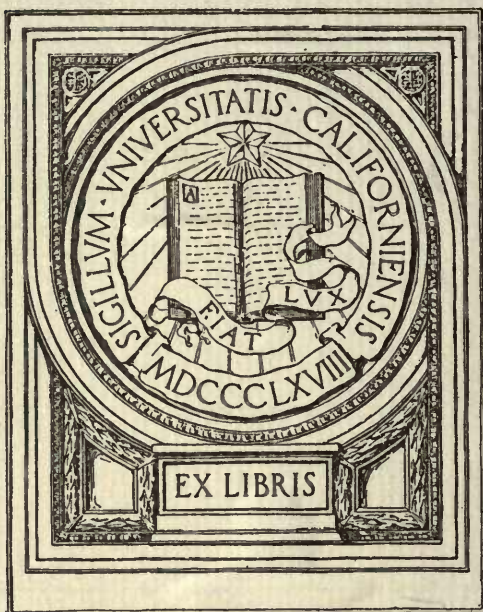


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The Life Cycle of Echinostoma revolutum (Froelich.)

THE LIFE CYCLE OF ECHINOSTOMA REVOLUTUM (FROELICH).

by

John C. Johnson

A THESIS

Contents

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1920

SUBMITTED IN PARTIAL SATISFACTION OF

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MAY 10, 1919

JOHN C. JOHNSON

VED BY:

J. H. Holmes
Daniel
L. J. L. L.
Hugh
L. J. L.
W. Cort

Chairman

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THE LIFE CYCLE OF ECHINOSTOMA REVOLUTION (THOUGHTS).

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SUBMITTED IN PARTIAL SATISFACTION OF

THE REQUIREMENTS FOR THE DEGREE

OF DOCTOR OF PHILOSOPHY IN THE

UNIVERSITY OF CALIFORNIA

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INTRODUCTION.

The Life Cycle of Echinostoma revolutum (Froelich.)

by

John C. Johnson

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At the suggestion of Professor W. W. Cort, the writer undertook in August 1917 to work out the excretory system of an echinostome cercaria which later proved to belong to Echinostoma revolutum (Froelich). After tracing the

The Life Cycle of Helicoverpa zea (Pieris)

by

John G. Johnson

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INTRODUCTION.

Although many different species of adult echinostomes have been recorded, nowhere in the literature do we find the description of all the stages of their life cycle. In 1909, Luh (1909, p. 65) clearly states that up to that time the life cycle was insufficiently known and that with a certainty no cercaria had been identified as belonging to a definite adult echinostome. The nearest approach to finding all the stages of the life cycle was made by Nicoll (1906, 1906a) and Lebour (1908) in their work on Echinostomum secundum Nicoll. However, these workers definitely state that no stage before the redia with cercariae inside were seen. Since that time neither in Europe nor America have all the missing stages been traced. This lack of information is due mostly to the complex life cycle. The chief difficulties involved are those of connecting exactly, by experimental feeding, the encysted agamodistome with the adult echinostome and of finding the exact species or genus of snail into which the miracidium will enter.

Knowledge concerning the entire excretory system of any stage of the life cycle of an echinostome is even less complete than that of the life history. This lack of knowledge is due largely to wrong methods of study which formerly consisted of using only preserved specimens.

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The third method was also experimental. It consisted of examining the ramifications of the tubules of the excretory system of the cercaria, work on this system in the redia was taken up. This led to the search for other stages suspected to exist in the life of this species. The species chosen proved to be favorable for both types of work.

METHODS OF STUDY.

The solution of the life cycle was undertaken in four ways. The first method was that of examining carefully a large number of snails, Physa occidentalis Tryon, from Stow Lake, Golden Gate Park, San Francisco, in which the cercariae were present to see if there might not be found other stages if studied during the entire year. Careful examination of four hundred of these snails showed 86-3/4 per cent were infected with either or both the encysted agamodistomes or rediae. In addition, one other stage, the daughter redia, previously never reported for echinostomes, was found.

The second method was experimental. It consisted of feeding large numbers of encysted agamodistomes to white mice, New Zealand rabbits, white leghorn chicks, and mongrel ducklings. They were all protected in every way from other trematode infections, the last two being incubator hatched and brooder raised. They were never allowed near water or soil, there being always a board floor in the brooder. Their food was also carefully selected. Negative results were obtained from the experiments with the mice, rabbits and chicks, but the ducklings gave positive results.

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The third method was also experimental. It consisted in hatching the echinostome eggs in Syracuse dishes in which most of the water was changed daily. Shortly before the miracidia were due to emerge, young snails were placed in the Syracuse dishes with the eggs. These young snails were raised from eggs in aquaria which in no way could have become infected. They were about six months old at this time.

The fourth method was that of examining the various suspected water birds from the lake from which all the snail were taken and particularly those birds which stay on the lake nearly or all the year around. The following water birds were examined: one specimen of Olor columbianus (Ord.); one of Anseranus semipalmata (Lath.); three mud hens, Fulica americana (Gmel); one shoveller duck, Spatula clypeata (Linn); one mallard, Anas platyrhynchos Linn; two ruddy ducks, Erismatura jamaicensis (Gmel.); and two bluebills or more accurately the American Scaup, Marila marila (Linn.). All but the American scaup gave negative results for echinostome. From one of these two ducks, adult echinostomes were obtained which proved to be the same species as those gotten from the experimentally fed ducklings.

The tracing of the excretory system of the cercaria was accomplished by using the method described by Cort (1918). This method of using living specimens for study by placing them under a No. 1 cover slip, although on the whole advantageous, has a decided disadvantage since most

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of the water must be withdrawn to slow down the movement of the animal. When a slight amount more of water is withdrawn, due to evaporation, the body wall quickly breaks in many places. For this reason great numbers of cercariae had to be studied before the system was completely worked out.

ACKNOWLEDGMENTS.

I wish here to express my thanks to Mr. Bryant Walker of Detroit, Michigan and Mrs. Oldroyd of Stanford University for identification of snail hosts; to Mr. John MacLaren, Superintendent of Golden Gate Park, for permission to obtain water-fowl in said park; to Mr. Charcotte of Golden Gate Park and those under his charge and to Mr. C. G. Budd, special game warden and policeman of San Francisco, for collecting and shipping the swans, mud hens and ducks; to Mr. F. H. Ballou, of the Department of Zoology, for collecting snails and other materials used in this study; to Dr. Joseph Grinnell and Mr. Tracy I. Storer, of the Museum of Vertebrate Zoology, for identification of vertebrate hosts; and to Mrs. Johnson for directing the experimental feeding of chicks and ducklings and for help in various ways.

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Eggs and Development of Miracidia

From adult specimens of Echinostoma revolutum found in the intestine of the duck, Marila marila (Linn.), about forty-five mature eggs were obtained, nearly all of which developed into miracidia. From adults of the same species raised experimentally in ducklings, several hundred eggs were also obtained, part of which did not mature since they were forced out by pressure from the uterus. The eggs from both sources were alike in color, shape and size variations as would be expected since the adults belong to the same species. They measured in length from 0.094 to 0.119 mm., the majority being about 0.108 mm. These figures fall within the range of variation given by Looss (1899 p. 679-689). His measurements show larger and smaller eggs than mine, which is to be expected since he measured eggs from more adults. The color of the egg is usually yellow or yellowish brown.

In order to watch the eggs from day to day, they were placed in syracuse dishes containing tap water. To keep the eggs in a favorable medium part of the water was changed daily. About fifteen eggs were placed in each dish in a room where the temperature varied little from 70° F.

At one end of the egg is usually to be found a slight thickening of the shell which appears of a darker color. At the other end is the operculum or cap. When the eggs emerge from this echinostome they are in the one cell stage (fig. 1). This condition can also be readily determined by studying the eggs while still in the uterus. Although little work has been done on echinostome eggs, it seems probable that the one cell stage

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of development at the time of emerging is a family characteristic. Looss' drawing (1896, fig. 92) clearly shows eggs of Echinostomum liliputanum in the one cell stage near the genital pore. Usually the two cell (fig. 2) and the four cell (fig. 3) stages are formed within the first twenty-four hours. During this time the yolk mass appears somewhat cellular. It is made up of two materials, one of opaque granules, the other of an oily and semi-transparent fluid. The granules are prominent and at this stage are numerous and small. These two materials seem to be mixed with each other making a medium whose nature is difficult to show in a drawing. As the number of cells of the miracidium increase the granules of the yolk material collect into large units but again decrease in prominence until by the twelfth day they have almost disappeared. By the seventh day the oily material has formed many well defined globules (fig. 7). On the second or third day the eight, ten and twelve cell stages are reached (fig. 4). On the fourth day about twenty cells are represented (fig. 5). On the sixth day the number of cells have increased to about thirty (fig. 6), each cell being somewhat smaller than in the stages where there are fewer cells. During this time the embryo remains quite distinct from the yolk mass, ^{although} the exact boundary line is sometimes difficult to determine. On the seventh day (fig. 7) angular epithelial cells of the miracidium are clearly distinguishable. On the eighth day (fig. 8), the condition differs from the preceding day principally in the great reduction of the granules of the yolk material. Also on

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this day the epithelial cells are less distinct. On the tenth day (fig. 9), the embryo has attained a shape which is somewhat like that of a fully developed miracidium, the nuclei of the epithelial cells are less distinct and the oily globules are fewer but larger in size. On the eleventh day (fig. 10), the embryo is still longer and on the posterior end a tail-like structure appears which possibly represents the region of the primitive germ balls. This projection disappears in a few days. The first movement of the embryo is also to be seen on this day, which consists of contraction and expansion at the anterior end. On the twelfth day (fig. 11), the movement has increased, while the muscular nature of the body wall has become evident. The oily globules are still fewer in number yet larger. At the end of two weeks (fig. 12), germ balls can be seen at the posterior end of the embryo miracidium, while the activity has still further increased. On the sixteenth day (fig. 13), the embryo is nearly as long as the egg, the eye spot has appeared and more germ balls are visible. For the first time flame cells are to be seen. They are two in number, one being more anterior than the other. Also the primitive digestive tract is visible. On the seventeenth day (fig. 14), the germ balls have increased to about twelve or fifteen in number, the primitive digestive tract is more clearly outlined, the epithelial cells are becoming quite opaque and thus the flame cells can hardly be seen. The activity of the miracidium has also greatly increased beyond that of the previous day. On the twentieth day (fig. 15), the embryo

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previous day. On the twentieth day (fig. 15), the embryo

has greatly increased in length, being now about 0.120 mm., but this is accompanied by a decrease in width. Because of this increase in length, the posterior end is often doubled back in the egg. The primitive digestive tract is larger and the germ balls are more conspicuous. For the first time the cilia on the surface of the body are clearly distinguished. The activity now is often violent, the miracidium lunging back and forth against the operculum. The egg is now ready to hatch. Figure 16 shows another mature miracidium also ready to hatch, in which the central nervous system is apparent.

I am inclined to believe that studies on the development of other echinostomes will show the above description of development to be quite characteristic of the family. This opinion is based upon the fact that distantly related families show quite similar development of the miracidium. Because of the opaque condition I was unable to determine whether the two flame cells are joined by short nearly straight capillaries or if the capillaries are long and much coiled. The excretory pores are located on each side near the posterior end. The excretory system of most miracidia seems to consist of but two flame cells and two capillaries. Looss (1896, pls. XI and XII) finds the excretory system of the miracidium of Gastrodiscus aegypticus (Cobbold), Gastrophylax gregarius Looss and "Distomum hepaticum variet. aegyptica", following this plan. Looss (1892, pl. XLX) again shows that in "Amphistomum subolavatum",

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A few minutes after figure 15 had been drawn, I was fortunate enough to observe the miracidium escaping from the egg. After many and vigorous lunges the operculum opened as if on a hinge (fig. 17). Within three seconds the whole miracidium was out and swimming vigorously about in search of its proper host. The operculum measures 0.023 mm. in diameter. Inside the newly hatched egg (fig. 17) is to be seen a considerable amount of waste and oily material. This material as well as the operculum is lost, however, inside of a few hours (figs. 18 and 18a).

Altho the echinostome eggs are much alike in shape they differ considerably in size. Even in the same species there is considerable variation. Perhaps the largest echinostome egg of unquestionable record is that of Pegosomum saginatum (Ratz), the length of which is 0.130 mm. and the width 0.089 mm., but even here there is great variation in size. One of the smallest echinostome eggs produced is by Monilifer spinulosus (Rud), measuring but 0.069 to 0.072 mm. in length by 0.048 to 0.050 mm. in width. Although variation in size of eggs is common to nearly all digenetic trematodes, yet no species seems to have greater variation than the records given for Echinostoma revolutum. The greatest length yet recorded for this species is by Looss (1899, p. 682), who has gotten the extreme measurement of 0.134 mm. Throughout the whole genus Echinostoma, however, the mean is not far from 0.110 mm. The great variation in size of eggs in

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Echinostoma revolutum suggests that Looss (1899, pp. 679-684) and others, have placed several species under this one name. This will be more carefully discussed under the heading of the adult echinostome.

Infection of Snails and Development of Mother-Rediae.

Young snails of Physa occidentalis were placed in syracuse dishes with the eggs of Echinostoma revolutum in which the miracidia were almost fully developed. These young snails were known to be free from any trematode infection since they were raised in small aquaria from eggs produced during the months of August and September 1918. To make doubly sure, many of the young snails were killed and carefully examined but all those examinations gave negative results.

At the time of the first experiments the snails were about six months old. Usually eight snails were placed in each syracuse dish with about fifteen eggs. During the first day almost all of the eggs were eaten by the snails but they passed ^{through} the digestive tract of the snails unharmed. They remained in the feces until they hatched, which occurred at the end of twenty-one days.

In one syracuse dish in which no young snails were placed, the movement of the miracidia outside the egg was studied. Their activity is much like other miracidia for about twenty-four hours. At the end of that time the vigorous activity quite rapidly subsides, followed in a short time by a breaking of the body wall and the extrusion of some of the contents.

Helicostoma revolutum suggests that Looss (1899, pp. 475-484) and others, have placed several species under this one name. This will be more carefully discussed under the heading of the adult Helicostoma.

Infection of Snails and Development of Mother-Nedias.

Young snails of Physa acicula were placed in Syracuse dishes with the eggs of Helicostoma revolutum in which the miracidia were almost fully developed. These young snails were known to be free from any trematode infection since they were raised in snail aquaria from eggs produced during the months of August and September 1918. To make doubly sure, many of the young snails were killed and carefully examined but all these examinations gave negative results.

At the time of the first experiments the snails were about six months old. Usually eight snails were placed in each Syracuse dish with about fifteen eggs. During the first day almost all of the eggs were eaten by the snails but they passed ^{the} the digestive tract of the snails unharmed. They remained in the faeces until they hatched, which occurred at the end of twenty-one days.

In one Syracuse dish in which no young snails were placed, the movement of the miracidia outside the egg was studied. Their activity is much like other miracidia for about twenty-four hours. At the end of that time the vigorous activity quite rapidly subsides, followed in a short time by a breaking of the body wall and the extrusion of some of the contents.

In the other syracuse dishes the miracidia must have penetrated the young snails almost immediately since they were never to be found free in the water except for a few minutes after hatching. The penetration of the young snail by the miracidium I was never fortunate enough to observe. Because of its large anterior papilla which is capable of being greatly retracted and then forcibly extruded, I judge that it would encounter little difficulty in piercing the thin body wall of the viscera or even the more rigid foot of the snail.

From time to time, these young snails were carefully examined to see what stage followed. All the evidence points to the fact that the miracidia metamorphose directly into rediae, which in this paper I shall call mother-rediae. On several occasions very small mother-rediae were obtained, measuring in length from 0.148 to 0.302 mm. After thirty-five days in the tissues of the young snails some mother-rediae had only increased 0.028 mm. beyond the length of the miracidium, thus being in all only 0.148 mm. long in its most contracted condition. The smallest contracted free daughter-redia ever seen measured 0.180 mm. in length, or 0.032 mm. longer than mother-rediae when five weeks old. If these young mother-rediae had been daughter-rediae instead then there would also have been present large rediae, which never were found even after the most careful examination. Also if I had missed a generation, and these mother-rediae were really daughter-rediae, then large numbers of daughter-rediae should have been found. But never were more than three found in a snail and that only once, the rest contained two

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or one mother-rediae or none. Also the shape at this time is somewhat different from the daughter-rediae. These four facts taken together make me feel certain that there is no intervening stage between the miracidia and the rediae found in the experimental snails.

The variation in the size of these small mother-rediae is due partially to the degree of contraction. They are more sensitive than when mature since they contract and expand if slightly interfered with on a slide. Figure 19 shows a mother-redia in four different shapes due to the degree of contraction. Figure 19a shows the mother-redia to be almost sac-shaped with no trace of the posterior protrusions. Figures 19b, c and d show the posterior protrusions becoming more prominent as the length increases. The blind intestine also shortens and lengthens with the body. The variation of the size of the blind intestine is characteristic at this stage of development.

Because of the opaqueness of the body of the young mother-redia, the germ balls could not be made out although they are undoubtedly as large and as numerous as they were in the miracidium.

How long it takes the mother-redia to develop to maturity and to produce another parthenogenetic generation is as yet undetermined but quite likely it is accomplished in about three months during the warmer weather.

The germ balls on the inside of the mother-rediae undoubtedly develop into daughter-rediae, but I cannot be certain whether there is more than one generation of daughter-rediae since this stage has not been followed throughout the entire year.

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their way into a single snail, which undoubtedly happens
 Rediae Containing Daughter-Rediae
 many times. Figure 28 shows a mother-redia containing

ten. In thirteen snails of Physa occidentalis, taken from
 Stow Lake, San Francisco, rediae with daughter-rediae inside
 were found. Although I have never obtained very small rediae con-
 taining daughter-rediae in these snails, and altho I have
 not traced the cycle of the daughter-rediae yet, I feel
 quite certain that there is only one such generation.
 Because of the fact that I believe only one generation of
 daughter-rediae to exist, I shall call the rediae enclosing
 daughter-rediae the mother-rediae. These mother-rediae,
 I feel quite certain, have been derived by metamorphosis
 from miracidia, as were the mother-rediae found in the
 young experimental snails.

The first evidence is that of the thirteen snails found
 to harbor the mother-rediae, eleven of these contained only
 a few rediae, and of these there were never more than four
 or five mother-rediae, usually less. In the two cases where
 mother-rediae were found in snails having many rediae pro-
 ducing cercariae, these mother-rediae were limited to
 three or four in number. Had there been more than one
 generation of daughter-rediae, then numerous rediae with
 daughter-rediae inside would likely be found since the
 daughter-rediae and germ balls inside of one rediae often
 exceed seventy. The second evidence is that one generation
 of daughter-rediae coming by metamorphosis from a single
 miracidium, is all that is necessary to produce the average
 number of rediae found in a single snail. In case of two
 or three hundred rediae being found in one snail, that could
 easily be explained by two, three or four miracidia finding

Rediae containing Daughter-Rediae

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or three hundred rediae being found in one snail, that could
easily be explained by two, three or four miracidia finding

their way into a single snail, which undoubtedly happens many times. Figure 26 shows a mother-redia containing ten daughter-rediae in which the pharynx and digestive sac is clearly distinguishable besides thirty-one fair sized germ balls and many smaller ones in the one and few cell stages. In another mother-redia were found seventy-one daughter-rediae and fair sized germ balls as well as many smaller ones.

When the daughter rediae emerge they measure from 0.180 to 0.250 mm. in length, depending mostly on the degree of contraction, and contain small germ balls (fig. 29). At the time of emerging the activity is usually quite great. The shape is nearly like that of a fully developed redia with quite prominent posterior projections, but the "collar" and birth pore are very small or entirely absent.

The daughter-redia stage was not found before December 1918, but this is readily explained by the fact that only those snails having a heavy infection were examined carefully since the material was so abundant. It is also likely that the daughter-redia stage is somewhat seasonal and thus the chance of finding it is greatly reduced.

The daughter rediae find their way out ^{through} the birth pore one at a time thus allowing room for other germ balls to increase in size.

This part of the life cycle differs from Fasciola hepatica since the latter has several generations of daughter-rediae while Echinostoma revolutum seems to have but one.

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Rediae Containing Cercariae.

produce the

The rediae that / cercariae of Echinostoma revolutum are, I believe, those that have emerged directly from the mother-rediae which were probably derived by metamorphosis from miracidia. In all structural characters the rediae producing daughter-rediae and the rediae producing cercariae, seem to agree at maturity.

The rediae are quite characteristic even though they vary greatly in size, shape, color, activity and number of cercariae and germ balls enclosed.

Rediae containing active or mature cercariae vary from 0.31 to 2.80 mm. in length, the average being about 1.60 mm. The smaller rediae contain few, usually only one active cercaria and a small number of germ balls. The larger ones may have as many as eleven active cercariae inside with perhaps seventy good sized germ balls, besides many other smaller ones. Active cercariae are nearly mature and always contain prominent concretions. The count of the active cercariae was often made upon this characteristic which was found to be wholly reliable. Occasionally a large redia may contain only one or two active cercariae and a few germ balls and on a very few occasions only two or three germ balls and no active cercariae. These I judge to be old rediae producing their last cercariae before final deterioration as several entirely empty and apparently lifeless rediae were seen. From fifty rediae taken at random the average number of active cercariae proved to be five with also at least fifty fair sized germ balls.

Radial Containing Oocytes.

produce the

The radial that / contains of follicles

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be five with also at least fifty fair sized germ balls.

This great variation in size is accounted for in two ways. First, that there is no very definite adult size and second, that mature cercariae are produced long before the rediae are full grown. They possibly continue to grow and to produce cercariae until the last of the germ balls are matured. I am inclined to think that the first explanation accounts for most of the variation.

The great variation in number of germ balls contradicts Ssinitzins theory (1911) that the number of cercariae and germ balls of a given species fall within a certain definite yet quite a large range. To a certain extent the number of germ balls is determined by the size of the redia, but there are plenty of exceptions.

The shape of the redia is usually that of a stocking when viewed from the side (figs. 26 and 27) and apparently straight when viewed dorsally or ventrally. Many other shapes may be found, however, as nearly ball-shaped, very long and slender, or even constricted in one or more places. The characteristic echinostome marks are present in all, however, if viewed from the proper angle. The paired posterior protrusions are usually located near the middle of the body. They extend ventrally, slightly laterally and protrude about one-half the width of the redia. They are rounded and non-muscular, apparently never moving in a forward direction. Upon these protrusions the redia usually rests when placed in water, the anterior end often swaying from side to side. At the anterior end a circular projection or "collar" is found. This "collar" is somewhat rigid and into it the neck of the redia may be partially withdrawn.

This great variation in size is accounted for in two ways. First, that there is no very definite adult size and second, that mature cercariae are produced long before the radia are fully grown. They possibly continue to grow and to produce cercariae until the last of the germ balls are matured. I am inclined to think that the first explanation accounts for most of the variation.

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Figures 24 and 25 show the elongated and contracted anterior end of the redia. Just back of the collar, to the left, to the right or dorsally the birth pore is located. It is usually quite prominent. The mouth is located at the anterior end, immediately followed by a pharynx which varies greatly in diameter due mostly to the size of the rediae. However, the average diameter is about 0.08 mm. The blind intestine is club-shaped and about twice the length of the diameter of the pharynx.

The color of the redia varies from almost a transparent condition to a heavy dark brown. The former condition is only to be seen in young or active rediae, the latter usually in inactive and apparently very old rediae. The light orange or light brown color which is the more common, is to be found in both the large and small, the young and old, the active and inactive rediae.

The activity as stated varies much, the greatest being in the younger rediae. In one case a newly freed daughter-redia measured only 0.180 mm. in its most contracted form (fig. 22), while extended it had a length of 0.405 mm. (fig. 23). There is, however, as stated no locomotion, rather only a swaying from side to side using the posterior protrusions as a pivot.

Because the variation is so great, some might ask if all belonged to one species. The answer is that without a question they all are the rediae of Rehinostoma revolutum. The two main proofs are that from every type of rediae the same cercaria emerged having its definite shape, size, number of spines and arrangement of excretory system and that in a single small pond there were found rediae of

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The activity as stated varies much, the greatest being in the younger radia. In one case a newly hatched daughter radia measured only 0.150 mm. in its most contracted form (fig. 22), while expanded it had a length of 0.408 mm. (fig. 23). There is, however, as stated no locomotion, rather only a swaying from side to side using the posterior projections as a pivot.

Because the variation is so great, some might say it all belonged to one species. The answer is that without a question they all are the radia of Enhydra tentaculata. The two main groups are that from every type of radia the same characters emerged having its definite shape, size, number of spines and arrangement of excretory system and

of the above discussed characters were found as in the sum-
total of the snails examined of this species.

The excretory system of the redia (fig. 31) is often difficult to see and I found it impossible to make out even under the very best microscopical condition. The most difficult part to make out proved to be the capillaries and smaller tubules at either end of the collecting tubules. The excretory pore is located on the side and slightly in front of the posterior projection of the body. Immediately underneath is a small bladder, which gives off two branches, the collecting tubes, one extending posteriorly and the other anteriorly. Close around the posterior projection eighteen flame cells were seen. No plan of branching or attachment of the capillaries could be made out due to the extreme coiling. At the anterior end, a short distance behind the intestinal sac seventeen flame cells were seen. These capillaries and accessory collecting tubes were also much coiled and so the pattern could not be determined here either: Possibly other flame cells are to be found at either end. It is quite probable that this condition of the excretory system prevails on both sides although in a given specimen it was never so seen. Other rediae, whose excretory system has been worked out show it to be bilateral and the pattern to be quite definite. This bilaterality is well illustrated by Looss (1896, fig. 153) in the redia of Cercaria distomatosa Sons. It also has its capillaries and flame cells arranged in groups of threes. He also shows the young redia of Amphistomum conicum R. When seen from the side the ventral sucker is often to be found

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 in the redia of Ceratomyxa discolorata Zoon. It also has the
 capillaries and flame cells arranged in groups of threes.

He also shows the young redia of Amphilectus echinus M.

of the middle of the body.

(fig. 130) arranged in a definite plan. Again Looss (1892, pl. XX, fig. 9) shows "*Amphistomum subclavatum*" to be bilateral, having two flame cells on a side. Cort (1918c, pl. VII, fig. 2) also finds *Cercariaeum mutabile* to be bilateral and as far as he could make out, with definite capillary arrangement. From this evidence it seems conservative to say that probably the excretory systems in all rediae are bilaterally symmetrical and may have a definite grouping of the capillaries and flame cells.

arranged in two alternate *Cercaria* altho the ventral ones

show more of a clumping than the alternating arrangement.

The fully developed cercaria of *Echinostoma revolutum*

These collar spines do not appear until perhaps the very

has a total length of from 0.82 to 1.25 mm., according to

last thing in the development of the cercaria. Often

the degree of contraction, averaging about 1 mm. when

were apparently mature cercariae found within the redia

moderately extended and from 0.19 to 0.30 mm. in width,

without these collar spines or at least only faintly

averaging about 0.25 mm. at its widest part. The body

developed. This probably explains why *Echinostoma* cercariae

alone varies from 0.39 to 0.63 mm. depending on the amount

of contraction; the tail from 0.43 to 0.62 mm. depending

The surface of the body is covered with spines.

Dorsally they extend to the back of the oral

or expansion of the body and tail there is an even greater

sucker. Ventrally they extend to the ventral sucker

range of variation. Generally the length of the body and

where they gradually taper to the tail, spines and

tail are about equal when moderately extended, each being

arrangement. Figure 130 shows the typical

about 0.50 mm. The width of the tail under average extension

the side of the cercaria, and the ventral suckers.

is about 0.05 mm. at the widest point. Actual variation in

They measure in this way.

the size of cercariae is not observable, the difference being

due entirely to the degree of contraction. The ventral sucker

of considerable size, the latter extending nearly

is somewhat larger than the oral sucker; the former measur-

to the posterior end, the latter ventral, the typical

ing on the average 0.094 mm. and the latter 0.072 mm. When

Echinostoma position, the oral sucker is about 0.025 mm. in

seen from the side the ventral sucker is often to be found

greatly extruded (fig. 44). It is located just back

(fig. 130) arranged in a definite plan. Again Leese (1892, pl. XX, fig. 9) shows "Amphistomum subolatum" to be bilateral, having two flame cells on a side. Gort (1918, pl. VII, fig. 2) also finds Gortystomum murale to be bilateral and as far as he could make out, with definite capillary arrangement. From this evidence it seems conservative to say that probably the excretory systems in all regiae are bilaterally symmetrical and may have a definite grouping of the capillaries and flame cells.

Ceraria

The fully developed ceraria of Bohlstonia revolutum has a total length of from 0.32 to 1.25 mm., according to the degree of contraction, averaging about 1 mm. when moderately extended and from 0.19 to 0.30 mm. in width, averaging about 0.25 mm. at the widest part. The body alone varies from 0.32 to 0.63 mm. depending on the amount of contraction; the tail from 0.43 to 0.62 mm. depending on the same condition. Occasionally in extreme contraction or expansion of the body and tail there is an even greater range of variation. Generally the length of the body and tail are about equal when moderately extended, each being about 0.50 mm. The width of the tail under average extension is about 0.05 mm. at the widest point. Actual variation in the size of ceraria is not observable, the difference being due entirely to the degree of contraction. The ventral sucker is somewhat larger than the oral sucker; the former measuring on the average 0.094 mm. and the latter 0.072 mm. When seen from the side the ventral sucker is often to be found greatly extended (fig. 44). It is located just back

of the middle of the body.

The number of collar spines is probably always forty-three. These spines have been counted on a large number of cercariae and that number seems to be specific. Although the possibility of missing count by one is easily understood by those who have attempted such counts, I feel quite safe in saying that the collar spines are forty-three in number. The ventral and lateral spines of the collar are from 0.016 to 0.018 mm. in length, being a little larger than the dorsal spines which are 0.014 mm. long. The spines are arranged in two alternate rows, altho the ventral ones show more of a clumping than the alterⁿation arrangement. These collar spines do not appear until perhaps the very last thing in the development of the cercaria. Often were apparently mature cercariae found within the radia without these collar spines or at least only faintly developed. This probably explains why echinostome cercariae have been ^{recorded} without the collar spines.

The surface of the body is partially covered with spines. Dorsally they extend just a short distance back of the oral sucker. Ventrally they reach well past the ventral sucker where they gradually lose their definite size, shape and arrangement. Figure 45 shows these spines as arranged on the side of the cercaria between the oral and ventral suckers. They measure in this region 0.006 mm. in length.

The digestive system (fig. 41) is quite easily seen and of considerable size, the intestinal caeca extending nearly to the posterior end. The mouth is slightly ventrad, the typical echinostome position. The pharynx is 0.035 mm. in length by 0.025 mm. in width, and is preceded by a prepharynx about

of the middle of the body.

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The surface of the body is partially covered with spines.

Dorsally they extend just a short distance back of the oral

sucker. Ventrally they reach well past the ventral sucker

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the side of the cercaria between the oral and ventral suckers.

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The digestive system (fig. 41) is quite coarsely seen and

of considerable size, the intestinal caeca extending nearly

to the posterior end. The mouth is slightly ventrad, the typical

echinostome position. The pharynx is 0.025 mm. in length by

0.025 mm. in width, and is preceded by a propharynx about

0.028 mm. in length. The oesophagus under average extension is about 0.14 mm. long while the bifurcation of the intestine is about 0.23 mm. in length.

The movement of the cercaria is accomplished in two ways, one of which is much slower than the other. The slower movement is leech-like and is used only on a surface. This is the only movement possible under the cover glass. When free in the water, however, the movement is vigorous. The body, which is concave ventrally between the suckers, is doubled in to the ventral sucker. The posterior end also is doubled in so that the body is almost in a ball. The tail then lashes vigorously back and forth, mostly in one plane, driving the cercaria at a high rate of speed but in no definite direction. The duration of this vigorous movement is usually less than twenty-four hours altho longer periods of activity have occasionally been seen. This movement is almost identical with that described by Cort for Cercaria trivolvis, Cort (1915, p. 37).

Excretory System

The excretory system of the cercaria of Echinostoma revolutum (fig. 47) proved to be extremely difficult to work out. The difficulties were due principally to two things. First to the fact that the entire body from the region of the pharynx to the posterior end is filled with cystogenous glands which are somewhat opaque. The longer the cercariae are free in the water the more opaque these glands become. The second difficulty is due to the complexity and progressive modification of the accessory

0.028 mm. in length. The oesophagus under average extension is about 0.14 mm. long while the bifurcation of the intestine is about 0.23 mm. in length.

The movement of the ceratris is accomplished in two ways, one of which is much slower than the other. The slower movement is leech-like and is used only on a surface. This is the only movement possible under the cover glass. When free in the water, however, the movement is vigorous. The body, which is constricted ventrally between the suckers, is doubled in to the ventral sucker. The posterior end also is doubled in so that the body is almost in a ball. The tail then lashes vigorously back and forth, mostly in one plane, driving the ceratris at a high rate of speed but in no definite direction. The duration of this vigorous movement is usually less than twenty-four hours although longer periods of activity have occasionally been seen. This movement is almost identical with that described by Gott for *Ceratris filivialis*, Gott (1913, p. 37).

Excretory System

The excretory system of the ceratris of *Leishmania* *revelans* (fig. 47) proved to be extremely difficult to work out. The difficulties were due principally to two things. First to the fact that the entire body from the region of the pharynx to the posterior end is filled with cystogenous glands which are somewhat opaque. The longer the ceratris are free in the water the more opaque these glands become. The second difficulty is due to the complexity and progressive modification of the necessary

collection tubules from the posterior end towards the oral region and to determining the exact place of attachment of the capillaries. Also the fact that only a few flame cells are likely to be active at a given time, some only during or after the bursting of the body wall, and the fact that a cercaria lasted only a few minutes added to the complexity of the situation. However, the abundance of material greatly offset these difficulties. In order to work out this system in this cercaria, one hundred and twenty snails were examined, of which eighty-six contained mature active cercariae. From these eighty-six snails probably over two thousand cercariae were studied before the complete ramifications of the tubules and the pattern could be made out. This one system was studied for a period of five consecutive weeks before this pattern was determined. the body. It may contrast

quite Since the limits of the bladder are poorly defined, I shall adopt the following nomenclature. The tubes in the tail I shall call the caudal division of the bladder, (1a); the commonly called bladder I shall call the muscular sac of the bladder (1b), which may or may not be divided into two parts as drawn in figure 47; the two large winding tubes joining the anterior end of the muscular sac of the bladder I shall designate as the muscular descending tubes of the bladder (1c), the divisions of the bladder containing the concretions I will term the concretionary descending tubes of the bladder (1d); the parts of the bladder attached to the concretionary descending tubes (1d) and extending backward to the posterior end of the body where each is joined

tubes contract and expand to about twice their normal size

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I shall designate as the muscular descending tubes of the
bladder (1c), the divisions of the bladder containing the
constrictions I will term the constrictional descending tubes
of the bladder (1d); the parts of the bladder attached to
the constrictional descending tubes (1d) and extending back-
ward to the posterior end of the body where each is joined

by three collecting tubules, will be called the ascending tubes of the bladder (1e); the collecting tubules are numbered 2a, 2b, 2c, and 2d, respectively, starting from the most anterior one; the accessory collecting tubules are designated as 3a, 3b, 3c, 3d, 3e, 3f, 3g and 3h respectively, also starting from the anterior end; the flame cells are numbered individually from one to twenty-four while their capillaries correspond, only with the "X" attached. The numbers of the flame cells appear on the left hand side, while the other designations are on the right side. However, since the two sides are alike it will be easy to transpose to the opposite side when necessary.

The muscular sac of the bladder (1b), is located at the extreme posterior end of the body. It may contract quite frequently to force out waste. It is usually of medium size and from its posterior end is given off a branch (1a), running into the tail which quickly subdivides into two parts. The subdivisions run nearly at right angles to the main branch, opening to the outside. Through these ^{excretory} pores all the body waste seems to pass. As stated, the muscular sac of the bladder usually appears in two parts connected by a narrow neck, but this is far from being constant, so these parts will be spoken of as forming a single part of the bladder (1b). The muscular descending tubes of the bladder (1c) join the muscular sac of the bladder (1b). These tubes of the bladder (1c) differ from the muscular sac of the bladder (1b), only in not being as muscular. Yet, I have seen these tubes contract and expand to about twice their average size

by three collecting tubules, will be called the ascending tubes of the bladder (1a); the collecting tubules are numbered 2a, 2b, 2c, and 2d, respectively, starting from the most anterior one; the necessary collecting tubules are designated as 3a, 3b, 3c, 3d, 3e, 3f, 3g and 3h respectively, also starting from the anterior end; the flame cells are numbered individually from one to twenty-four while their capillaries correspond, only with the "X" attached. The numbers of the flame cells appear on the left hand side, while the other designations are on the right side. However, since the two sides are alike it will be easy to transpose to the opposite side when necessary.

The muscular sac of the bladder (1b), is located at the extreme posterior end of the body. It may contract quite frequently to force out waste. It is usually of median size and from its posterior end is given off a branch (1a), running into the tail which quickly subdivides into two parts. The subdivisions run nearly at right angles to the main branch, opening to the outside. Through the pores all the body waste seems to pass. As stated, the muscular sac of the bladder usually appears in two parts connected by a narrow neck, but this is far from being constant, so these parts will be spoken of as forming a single part of the bladder (1b). The muscular descending tubes of the bladder (1c) join the muscular sac of the bladder (1b). These tubes of the bladder (1c) differ from the muscular sac of the bladder (1b), only in not being as muscular. Yet, I have seen these tubes contract and expand to about twice their average size

nearly up to the ventral sucker. In the region of the acetabulum the coiling of the muscular tubes of the body (1c) largely ceases, and from there to the region of the pharynx the tubular descending division of the bladder widen considerably. Inside of these tubes are to be found many prominent opaque concretions. This part is non-muscular and is thus quite distinct from the muscular tubes of the bladder (1c) and so is designated (1d). The concretions are small at the anterior end becoming larger and larger until the region of the forking of the intestine is reached when again they gradually become smaller. These concretions I believe to be gradually and continuously formed from the waste liquid, enlarging as they are pushed farther down the concretionary tubes of the bladder (1d). Why they again decrease in size, I cannot determine, but that they do is certain and that wastes pass out only in liquid condition is almost equally certain. Evidently the concretions are produced about as fast as dissolved and eliminated since I have never seen an active cercaria without these concretions filling this entire part of the bladder. In the region of the anterior end of the pharynx these tubular divisions of the bladder turn completely around forming a very characteristic area (fig. 47, t.a.). Here the ascending tubes of the bladder (1e) join the concretionary tubes of the bladder (1d). The difference between these two divisions of the bladder is apparently only physiological, i.e., in terms of the presence or absence of concretions and the diameter of the tubes. These latter divisions as

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stated are the ascending tubes of the bladder (1e). These divisions of the bladder pass ventral to the concretionary tubes of the body (1d), at the anterior end but later come to lie on the outside of and parallel to it. In the region of the posterior end of the ventral sucker, a collecting tubule (2a), joins the ascending tubes of the bladder (1e). This collecting tubule is joined shortly by a bulb-like accessory collecting tubule (3c), into which three capillaries enter that drain the wastes by means of three flame cells from the region of the acetabulum. A short distance anteriorly three other capillaries join this collecting tubule (2a). These capillaries unite singly some distance apart, to the collecting tubule. However, we might consider that the part of the tubule between capillaries 4x and 6x represents the accessory collecting tubule (3b). This seems probable because the accessory collecting tubule (3b), is reduced to a mere bulb and even here the capillaries do not join exactly at one place. At the anterior end of the collecting tubule (2a), three other capillaries are received which drain the wastes from the oral region. Here again the accessory collecting tubule (3a), has either ceased to be or it exists as the tubule between flame cells two and three. In this latter group the capillaries are even farther apart than the ones forming the group just preceding. This loss or modification of the accessory collecting tubules 3a and 3b is shown graphically by comparing text figure No. 1 with figure 47.

stated are the ascending tubes of the bladder (1e). These divisions of the bladder pass ventral to the constrictor tubes of the body (1d), at the anterior end but later come to lie on the outside of and parallel to it. In the region of the posterior end of the ventral sucker, a collecting tubule (2a), joins the ascending tubes of the bladder (1e). This collecting tubule is joined shortly by a bulb-like accessory collecting tubule (3a), into which three capillaries enter that drain the wastes by means of three flame cells from the region of the oesophagus. A short distance anteriorly three other capillaries join this collecting tubule (2a). These capillaries unite singly some distance apart, to the collecting tubule. However, we might consider that the part of the tubule between capillaries 4x and 6x represents the accessory collecting tubule (3b). This seems probable because the accessory collecting tubule (3b), is reduced to a mere bulb and even here the capillaries do not join exactly at one place. At the anterior end of the collecting tubule (2a), three other capillaries are received which drain the wastes from the oral region. Here again the accessory collecting tubule (3a), has either ceased to be or it exists as the tubule between flame cells two and three. In this latter group the capillaries are even farther apart than the ones forming the group just preceding. This loss of modification of the accessory collecting tubules 2a and 3b is shown retrospectively by comparing text Figure No. 1 with Figure 4x.

Thus to collecting tubule (2a) join three groups of three flame cells each, directly or indirectly, by accessory collecting tubules.

At the posterior end of the body, the ascending tube of the bladder (1e) receives three collecting tubules (2b, 2c, and 2d). One of these collecting tubes (2b) is considerably longer than the others. It receives two sets of three capillaries and flame cells, numbers 10, 11, 12 and 13, 14, 15. The most anterior group of capillaries arises nearly from the same point and drain the region at the posterior end of the acetabulum, while the other set is just a short distance behind, each capillary being attached singly. If the accessory collecting tubule for the first group exists it may be said to be between the capillaries 11x and 12x, while the latter group might be said to have for its accessory collecting tubule the part between 13x and 15x. Another collecting tubule (2c), if such can be said to exist, receives a very short accessory collecting tubule (3f), which in turn receives three capillaries almost uniting at the same point. The flame cells in this group are numbers 16, 17 and 18 and are located just behind the group previously mentioned, being about half way between the acetabulum and the posterior end of the body. The other collecting tubule (2d), is very short. Into it flow the wastes of the accessory collecting tubules (3g and 3h). To each one of these after much coiling join the capillaries of flame cells 19, 20, 21 and 22, 23, 24. anterior to the capillaries of the first group are the groups on the acetabulum and the collecting tubule. At the anterior end of the body of

Thus to collecting tubule (2a) join three groups of three flame cells each, directly or indirectly, by necessary collecting tubules.

At the posterior end of the body, the ascending tube of the bladder (1a) receives three collecting tubules (2b, 2c, and 2d). One of these collecting tubules (2b) is considerably longer than the others. It receives two sets of three capillaries and flame cells, numbers 10, 11, 12 and 13, 14, 15. The most anterior group of capillaries arises directly from the same point and drains the region at the posterior end of the neotubulum, while the other set is just a short distance behind, each capillary being attached singly. If the necessary collecting tubule for the first group exists it may be said to be between the capillaries 11x and 12x, while the latter group might be said to have for its necessary collecting tubule the part between 12x and 13x. Another collecting tubule (2c), if such can be said to exist, receives a very short necessary collecting tubule (31), which in turn receives three capillaries almost uniting at the same point. The flame cells in this group are numbers 16, 17 and 18 and are located just behind the group previously mentioned, being about half way between the neotubulum and the posterior end of the body. The other collecting tubule (2d), is very short. Into it flow the wastes of the necessary collecting tubules (2g, and 2h). To each one of these after much coiling join the capillaries of flame cells 19, 20, 21 and 22, 23, 24.

Thus the ascending tubes of the bladder (19) are joined on each side by four collecting tubules. One receives three sets of three flame cells each; two receive two sets each, and one only one set. On each side of the body are twenty-four flame cells. The formula for this system then is "2x8x3", totalling forty-eight flame cells, according to the plan used by Looss (1894, p. 68) and lately adopted by Cort (1919, p. 2). There are no flame cells found in the tail. The anterior half of the body contains only six flame cells on each side while the posterior half has eighteen. In terms of the cercaria this arrangement is hard to explain but in the light of the adult echinostome the number at either end is quite readily understood. In the adult (fig. 48) the region of the body back of the ventral sucker is several times longer than that anterior to it. Since I believe the plan of the excretory system of the cercaria is essentially the same as that of the adult, it is plain that a stretching of this system to meet the adults growth at the posterior end would result in a uniform distribution of the flame cells thruout the entire body when the worm is full grown.

As stated previously a significant progressive modification of the attachment of the capillaries is noticeable throughout the cercaria. At the posterior end of the body the groups of three capillaries join at a common point on the accessory collecting tubule and form very definite capillary groups. The farther anterior the capillaries join the more widely separated are the groups on the accessory collecting^{tubule}/or collecting tubule. At the anterior end, unless the plan of

Thus the ascending tubes of the bladder (19) are joined on each side by four collecting tubules. One receives three sets of flame cells each; two receive two sets each, and one only one set. On each side of the body are twenty-four flame cells. The formula for this system then is "2x8x5", totaling forty-eight flame cells, according to the plan used by Jodas (1924, p. 68) and lately adopted by Gort (1919, p. 8). There are no flame cells found in the tail. The anterior half of the body contains only six flame cells on each side while the posterior half has eighteen. In terms of the cercaria this arrangement is hard to explain but in the light of the adult echinostome the number at either end is quite readily understood. In the adult (fig. 4) the region of the body back of the ventral sucker is several times longer than that anterior to it. Since I believe the plan of the excretory system of the cercaria is essentially the same as that of the adult, it is plain that a stretching of this system to meet the adult growth at the posterior end would result in a uniform distribution of the flame cells throughout the entire body when the worm is fully grown.

As stated previously a significant progressive addition of the attachment of the apophyses is noticeable throughout the cercaria. At the posterior end of the body the groups of three apophyses join at a common point on the accessory collecting tubule and form very definite caudal groups. The farther anterior the apophyses join the more widely separated are the groups on the accessory collecting tubule. At the anterior end, unless the plan of

arrangement of the capillaries into threes were known thruout the rest of the body one would certainly say that each joined ^{accessory} the/collecting tubule or the collecting tubule singly instead of in threes. However, knowing this grouping into threes at the posterior end, it is not difficult to make the proper association here. This widening of the distance between the attachment of the capillaries in a group is accounted for by the gradual loss of the accessory collecting tubules or by the merging of the accessory collecting tubule and the collecting tubule into one.

These groups of three flame cells are arranged dorsally and ventrally in a definite way. The most anterior group is essentially a dorsal group appearing quite close to the upper surface. The next group of threes is a ventral one, the next one is dorsal, the next ventral and so on to the posterior end. The dorsal-ventral arrangement of the last two groups, however, I cannot be sure of because of their much coiling, yet I am reasonably certain that they are so arranged. That arrangement is probable if the entire body is to be drained equally. Again within the group of threes there is a definite arrangement. Starting at the anterior end the first flame cell is dorsal, the next ventral, the next dorsal; then in the next group of threes the first is ventral, the next dorsal, the next ventral, and so on. This again is a logical arrangement if dorsally and ventrally the body is to be equally well drained of wastes. These two plans, or some modification, I should expect to find in all cercariae and adults but as yet I believe it has never been reported.

From a study of the literature and the drawings of the excretory systems of cercariae that have been worked out, and

arrangement of the capillaries into three were known through the rest of the body and would certainly say that each joined the collecting tubule of the necessary collecting tubule and the of in three. However, knowing this grouping into three at the posterior end, it is not difficult to make the proper association here. This widening of the distance between the attachment of the capillaries in a group is accounted for by the gradual loss of the necessary collecting tubules or by the merging of the necessary collecting tubules and the collecting tubule into one.

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From a study of the literature and the drawings of the excretory systems of cestodes that have been worked out, and

from my own work, it seems probable that there is definite grouping of flame cells and their capillaries connecting with the accessory collecting tubules, and that each group though modified thru increase, reduction or loss of parts has come from the mitotic division of a single flame cell. In some cercariae as Schistosoma japonicum or Cercaria douthitti the capillary groups have not yet arisen since the capillaries are arranged singly, but I should expect to find in the adult worm each capillary represented by a group of flame cells.

In Echinostoma revolutum the groups are already present so in the adult I should expect to find the same number of flame cells.

The excretory system of the cercaria of Echinostoma revolutum has been modified somewhat and is hard to interpret as a definite unified arrangement thruout. This theory of the formation of capillary groups was first given by Looss (1894) and later accepted by Cort (1918a). Even in 1881 (pl. 1, fig. 4) Fraipont shows the formation of two flame cells by mitotic division, one on the left and the other on the

right. In the cercaria of Echinostoma revolutum sometimes the collecting tubules and again the accessory collecting tubules are much reduced or have entirely disappeared as shown in figure 47, 3c. This reduction or loss is likely due to several things, which might all be summed up by calling it adaptation to the position they occupy in the cercaria's body or the position they will eventually occupy in the body of the adult echinostome.

The figure following represents graphically what I consider to be the generalized system of an echinostome cercaria from which the present system probably arose. The comparison of this diagram with figure 47, illustrates a method by which the cap-

from my own work, it seems probable that there is definite
grouping of flame cells and their capillaries connecting with
the accessory collecting tubules, and that each group though
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from the mitotic division of a single flame cell. In some
organisms as Scaphinotus japonicus or Gerrusia chusidii
the capillary groups have not yet arisen since the capillaries
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where each capillary represented by a group of flame cells.
In Scaphinotus japonicus the groups are already present so in
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The figure following represents graphically what I considered
to be the generalized system of an echinostome cercaria from
which the present system probably arose. The comparison of this
diagram with figure 47, illustrates a method by which the cap-

illary grouping of a system could be progressively modified until the exact pattern is somewhat obscured.

The drawing (text fig. No. 1) shows particularly what I think has happened to the accessory collecting tubule (3c), to which are attached the capillaries draining flame cells seven, eight and nine. Compare with figure 47 as it really appears. As shown graphically this accessory collecting tubule is quite long whereas in the actual specimen I think it is reduced to a mere bulb, to which the capillaries join. In case of the accessory collecting tubule (3b) shown graphically to which are attached capillaries 4x, 5x, and 6x ⁱⁿ we find that/the drawing this accessory collecting tubule has entirely disappeared or perhaps better is stretched out between these capillaries. The same condition exists in case of the accessory collecting tubule of capillaries 1x, 2x and 3x. Near the posterior end of the ascending tubular division of the bladder (1e), are joined by collecting tubules (2b and 2c), one on the left and the other on the right hand side of each division of the bladder. The one on the right side (2b) receives, as shown graphically, two accessory collecting tubules 3d, 3e, which in figure 47 are entirely absent or are stretched out between 10x, 11x, 12x, and 13x 14x, and 15x respectively. The collecting tubule on the left (2c) merges directly into accessory collecting tubule (3f), as shown graphically and in the drawing has ceased to exist unless it is to be found between the capillaries (17x and 18x). The last collecting tubule, (2d), in the graph and in the living specimen is short, to which join accessory collecting tubules (3g and 3h). Thus it seems what I have suggested as the primitive pattern has been con-

illary grouping of a system could be progressively modified until the exact pattern is somewhat obscured. The drawing (text fig. 10-1) shows particularly what I think has happened to the necessary collecting tubule (20) to which are attached the capillaries draining flame cells seven, eight and nine. Compare with figure 47 as it really appears. As shown graphically this necessary collecting tubule is quite long whereas in the actual specimen I think it is reduced to a mere bulb, to which the capillaries join. In case of the necessary collecting tubule (20) shown graphically to which are attached capillaries 4x, 5x, and 6x we find that the drawing this necessary collecting tubule has entirely disappeared or perhaps better is stretched out between these capillaries. The same condition exists in case of the necessary collecting tubule of capillaries 1x, 2x and 3x. Near the posterior end of the ascending colubular division of the bladder (10), are joined by collecting tubules (20 and 20'), one on the left and the other on the right hand side of each division of the bladder. The one on the right side (20) receives, as shown graphically, two necessary collecting tubules 24, 25, which in figure 47 are entirely absent or are stretched out between 10x, 11x, 12x, and 13x 14x, and 15x respectively. The collecting tubule on the left (20') merges directly into necessary collecting tubule (21), as shown graphically and in the drawing has seemed to exist where it is to be found between the capillaries (17x and 18x). The first collecting tubule (24) in the graph and in the living specimen is short, to which join necessary collecting tubules (22 and 23). Thus it seems that I have suggested as the primitive pattern has been con-

siderably modified possibly to meet the shape and needs of the cercaria or of the adult echinostome.

The study of the development of the bladder in the cercaria of Echinostomum revolutum proved to be interesting and gave some definite results. The first appearance of the bladder or any part of the excretory system was seen in a germ ball 0.134 mm. long and 0.104 mm. wide (fig. 37). It had just commenced to change from the typical round germ ball. At this time two widely separated tubes extending nearly the entire length of the body are present. At the anterior end the tubes appear to end in flame cells which could not be clearly distinguished, due to the lack of movement of their cilia. Each tube clearly must function independently of the other since the two excretory pores are now 0.045 mm. apart. When the embryo reaches a length of 0.280 mm. the suckers are distinct; the digestive system is fairly well developed; the tail has commenced to differentiate from the body, and the excretory pores are closer together being only 0.018 mm. apart (fig. 38). When the embryo is 0.360 mm. long the digestive system is complete. At this time the inner surface of the walls of the excretory tubes nearly touch each other (fig. 39) a short distance above the excretory pores. The tail is now quite decidedly differentiated from the body. At about one-fourth the distance from the base of the body to the end of the tail the excretory tubules bend almost at right angles and empty laterally. Figure 42 shows the right half of this primitive muscular bladder in various shapes, drawn within a few seconds of each other. These swellings or bulbs give evidence

slightly modified possibly to meet the shape and needs of the oostegia or of the adult echinostoma.

The study of the development of the bladder in the oostegia of Echinostoma revolutum proved to be interesting and gave some definite results. The first appearance of the bladder or any part of the excretory system was seen in a germ ball 0.134 mm. long and 0.104 mm. wide (fig. 37). It had just commenced to change from the typical round germ ball. At this time two widely separated tubes extending nearly the entire length of the body are present. At the anterior end the tubes appear to end in flame cells which could not be clearly distinguished, due to the lack of movement of their cilia. Each tube clearly most function independently of the other since the two excretory pores are now 0.045 mm. apart. When the embryo reaches a length of 0.280 mm. the suckers are distinct; the digestive system is fairly well developed; the tail has commenced to differentiate from the body, and the excretory pores are clearly together being only 0.018 mm. apart (fig. 38). When the embryo is 0.350 mm. long the digestive system is complete. At this time the inner surface of the walls of the excretory tubes nearly touch each other (fig. 39) a short distance above the excretory pores. The tail is now quite decidedly differentiated from the body. At about one-fourth the distance from the base of the body to the end of the tail the excretory tubules bend almost at right angles and empty laterally. Figure 40 shows the right half of this primitive muscular bladder in various stages, drawn within a few seconds of each other. These swellings or bulges give evidence

of a process similar to peristalsis in the elimination of excretory waste as well as showing in this early stage that the bladder is quite decidedly muscular. When the embryo is 0.710 mm. long, the final shape of the cercaria is nearly attained. In this stage the union of the two tubules of the primitive muscular bladder is partially accomplished (fig. 40) just at the juncture of the body and tail. At 0.765 mm. in length (fig. 41) the process of union is nearly completed extending both into the body and tail. Thus the tubule found in the tail of mature cercariae is really a part of the bladder. Principally upon this data in regard to the bladder tubules in the tail Ssnitzin (1911), based his theory that the body proper of many cercariae really extends to the region of the excretory pores in the tail and not to where the slender part ordinarily called the tail joins the body. He then holds that the true tail is an outgrowth from tissue found just posterior to and between the excretory pores. There is considerable evidence, aside from the work of Ssnitzin to uphold this theory. Loos (1896, figs. 147, 155, 172, 173, 174) shows that in both monostomes and distomes such a bladder formation takes place. Also Loos (1892, pl. XX) shows several stages in the development of an amphistome cercaria portraying the same development of the bladder. From this evidence it seems to me quite logical to say that the body proper of such cercariae extends to the excretory openings on the side of the tail and that the true tail extends only from this point on.

Since the bladder sac is derived from the union of two tubes in the embryo, then certainly, if necessary, they could unite for a longer distance and form a much larger

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bladder. Also since the muscular descending tubes (1c), have the power of contraction and expansion it is obvious that to limit the bladder to the muscular sac is not correct. Also since the concretionary tubes of the bladder (1d) are continuations of the muscular tubes (1c), and since the ascending tubes (1e) are directly continuous with the concretionary tubes (1d), then that all these parts form the complete bladder seems to me to be the proper conception. tubules, accessory collecting tubules,

Nowhere is there found a record of the complete analysis of the excretory system of any stage of an echinostome. The nearest approach is the work of Looss (1894, fig. 191), in which he describes this system of the cercaria, which he believes to belong to Echinostoma revolutum (= Distomum echinatum). This cercaria, however, is not the cercaria of Echinostoma revolutum as will be proved under the discussion of the adult. As far as he goes, the smaller tubules and capillaries as well as the large tubules, divisions of the bladder and excretory pores, agree with the cercaria of Echinostoma revolutum. The posterior part of the excretory system he fails to show in detail. This failure can now readily be understood because of the cramped condition of the tubules and the density of the cystogenous glands. The anterior arrangement of the tubes of the bladder is nearly the same as in the cercaria of Echinostoma revolutum. The only difference is that at the anterior end the triangular arrangement of the tubes of the bladder as they bend to proceed posteriorly is not present in Looss' form. Lebour (1912, pl. XXXVIII)

bladder. Also since the muscular descending tubes (1a), have the power of contraction and expansion it is obvious that to limit the bladder to the muscular sac is not correct. Also since the constrictional tubes of the bladder (1b) are contractions of the muscular tubes (1c), and since the ascending tubes (1a) are directly continuous with the constrictional tubes (1b), then that all these parts form the complete bladder seems to me to be the proper conception.

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shows three cercariae in which the several divisions of the bladder as far as worked out, agree with the bladder of the cercaria of Echinostoma revolutum.

Faust (1917, and 1918) describes four new species of Echinostoma cercariae, Cercariae trisolentata, Cercaria biflexa, Cercaria chisolentata and Cercaria acanthostoma. He shows parts of the excretory system of each of these species but in no one does he find a definite pattern for the collecting tubules, accessory collecting tubules, capillaries and flame cells. Even the part which I have called the complete bladder he has described very differently in his forms. The excretory system of the digenetic trematode is quite conservative. Wherever the excretory system for different members of the same family has been worked out a marked uniformity is found. Loess (1894, pl. VIII, figs. 157 and 163) found two distomes, Opisthoglyphe ranae (Froelich) and Haplometra cylindriacea (Zeder) built on the "2 x 6 x 3" plan. Cort (1917) found four folk-tailed cercaria, Cercaria douthitti, Cercaria emarginatae, Cercaria douglasi and Schistosoma japonicum, with the flame cells arising singly. This quite probably means that the excretory system in the folk-tailed cercariae is different in number of flame cells from the adults. Each flame cell in the cercariae probably represents a group of flame cells in the adult. Since the echinostomefamily is so uniform in regard to other characters, it seems very improbable that such a conservative system as the excretory should vary greatly. The echinostome excretory systems described by Faust are almost entirely different from those

shows three cercariae in which the several divisions of the bladder as far as worked out, agree with the bladder of the cercaria of Schistosoma revolutum. Faust (1914 and 1918) described four new species of Schistosoma cercariae, Schistosoma trilineatum, Schistosoma biflexa, Schistosoma chalcidense and Schistosoma acanthostoma. He shows parts of the excretory system of each of these species but in no one does he find a definite pattern for the collecting tubules, accessory collecting tubules, capillaries and flame cells. Even the part which I have called the complete bladder he has described very differently in his forms. The excretory system of the digenetic trematode is quite conservative. However the excretory system for different members of the same family has been worked out a marked uniformity is found. Jones (1924, pl. VIII, figs. 127 and 128) found two distomes, Colpistomus alpinus (Yoccoz) and Haplometes cylindricus (Zeder) built on the 2 x 3 x 3" plan. Gort (1914) found four folk-tailed cercariae, Cercaria douvillei, Cercaria emarginata, Cercaria douvillei and Schistosoma japonicum with the flame cells arising singly. This quite probably means that the excretory system in the folk-tailed cercariae is different in number of flame cells from the adults. Each flame cell in the cercariae probably represents a group of flame cells in the adult. Since the schistosomatid family is so uniform in regard to other characters, it seems very improbable that such a conservative system as the excretory should vary greatly. The schistosomatid excretory systems described by Faust are almost entirely different from those

described by Looss (1894), Lebour (1912),^{and} Cort (1915) and from that of Echinostoma revolutum. Faust makes the following statement concerning the excretory system of echinostomes. "This family of distomes is characterized by simplicity of detail in the excretory system except at the head of the main lateral vessel". From my study of the cercaria of Echinostoma revolutum I am inclined to think that, just the opposite is true. Certainly it is very complex in this one species and since the excretory system is so conservative I can hardly believe the species of the Echinostomidae differ much on fundamental points. I even venture that when this system is studied in detail in more echinostomes the detailed arrangement of parts will be found to be quite similar in pattern. The parts of the excretory system found in the tail of Echinostoma revolutum, altho very simple in arrangement were found hard to work out on account of the deceptive appearance of the muscles in this region. This part of the excretory system of Echinostoma revolutum agrees with the description by Looss (1894, fig. 191), by Lebour (1912, pl. XXVIII, figs. 9, 13, 17) and by Cort (1915, figs. 39 and 43). This makes a total of at least seven echinostomes showing this characteristic arrangement of the bladder tubules in the tail of the cercariae. The four echinostome cercariae described by Faust differ decidedly on this characteristic from any of the above. They also differ much from each other. He shows none of them with excretory pores in the tail. The excretory system in the tail of Cercaria trisolinata is shown as a single tube. In comparison parts in the tail of echinostomes exists as described by

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he states this for Cercaria biflexa, (1917, p. 79). "The excretory tube in the tail is a single median tube for about two-fifths of the way distad, at which point it forks and continues double the remainder of the way distad, with numerous cross anastomoses. It does not open to the outside on either side or end". The excretory system in the tail of Cercaria acanthostoma Faust finds to be still different as is shown by the following quotation. "The excretory system in the tail is confined to a long sac-like reservoir, extending the entire length of the organ without any definite wall or lining. Near the proximal end it frequently bulges out on each side to form a lateral reservoir". He shows this sac-like reservoir in the tail to be fully four times the size of the muscular sac of the bladder. Cercaria chisolenata, he finds to be somewhat like Cercaria trisolenata altho the ending of the excretory tube is not quite so definite. I feel quite certain that he confused the tail excretory parts with the tail muscles. This statement is borne out by the fact that in Cercaria chisolenata (1918, fig. 9) he shows the tube in the tail and the muscles of the tail with the same type of line and then loses the excretory tube in the muscles. This apparent extension of the excretory tube in the tail as shown in Cercaria chisolenata and Cercaria biflexa, I have observed in the cercaria of Echinostoma revolutum many times but upon a more careful study the two excretory tubes and pores could also be seen. This proved to be one of the most difficult points to make sure about because of these deceptive muscles. That the wide variety of excretory parts in the tail of echinostomes exists as described by

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Faust, seems very improbable in such a well defined family and especially so since Looss, Lebour, Cort and myself have found a uniform type with two excretory pores in the tail.

Nowhere in the middle or posterior parts of three of his cercariae does Faust find flame cells. That they exist there I feel quite positive. The failure to see flame cells and tubules in these regions is probably due to the heavy cystogenous glands in these three species. Only at the anterior end where there are no cystogenous glands does he find the flame cells. In Cercaria acanthostoma, however, he shows flame cells directly connected singly with tubes which are equivalent in the other species to the anterior tubes of the bladder. That these flame cells join directly to the tubular division of the bladder is improbable since in no cercaria where the excretory system has been carefully and completely worked out does this occur. Rather do the flame cells by means of their capillaries, unite with accessory collecting tubules.

At the anterior end in each of these four new echinostome cercariae described by Faust, he shows three flame cells on a side. These three flame cells are probably present in all echinostome cercariae. Their arrangement and attachment is probably a family characteristic. I feel quite sure, however, that these three flame cells do not unite with the concretionary tubes of the bladder as shown in Cercaria trisolinata and Cercaria chisolinata or even as in Cercaria acanthostoma. As stated above, capillaries are not known to unite with parts of the bladder. The arrangement and attachment of these three anterior flame cells as shown in Cercaria biplexa (Faust 1917, fig. 138) is much like the

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cercariae of Echinostomum revolutum and "Distomum echinatum" as described by Looss. But even in Cercaria biflexa I am inclined to believe that the tubule to which the three anterior flame cells are attached does not bend forward and join the tube of the bladder but proceeds much farther posteriorly, joining the tube of the bladder in the region of the acetabulum (fig. 47, 2a). The fine capillaries shown in Cercaria biflexa (Faust, 1917, fig. 135) joining the tubes of the bladder is an improbable arrangement also. These capillaries are probably equivalent to the branching of the tubes of the bladder as shown by Lebour (1912, pl. XXVIII, fig. 9, 13, 17).

Concerning any of the criticisms of Faust's work, I will say in fairness to him, that since none of his species have been studied, I may have carried my criticisms based on comparison too far. It must be said, however, that his arrangement of the excretory parts violates some of the most fundamental homologies of excretory systems. Also since Faust's detail is so lacking, the conclusion is reached that he really did not completely solve the pattern of the excretory system of any one of the four echinostome cercariae.

Because of the numerous flame cells, the complexity of the arrangement of the collecting tubules and accessory collecting tubules and the definite arrangement into capillary groups thruout the body, it seems quite probable that the excretory system of the echinostome cercariae represents much more closely the adult condition than the condition found in the schistosomes or fork-tailed cercariae, where the flame cells arise singly, are few in number and

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The great knowledge of the excretory system of trematodes as stated is comparatively meager. In nearly every cercaria described the bladder and larger tubules are shown, whereas the collecting tubules, accessory collecting tubules, capillaries and flame cells are missing or nearly so. This is, as stated before, due to working on preserved material. But even tho the larger parts of the system have been long known, yet for considerable time they were confused with blood vessels, parts of the digestive tract, the oviduct and other parts of the genital system (Fraipont, 1880, pp. 415-420). The flame cell itself was perhaps first seen by Bütschli in 1879, so it is impossible that earlier researchers could have conceived of a unified system. Even after the flame cells and capillaries had been found, they were considered for a time as distinct from the larger tubules and bladder. That this confusion could readily exist can now be well understood, because of the minuteness and complexity of the parts of this system.

In reviewing the literature on excretory systems of cercariae that have been completely worked out this conclusion, I believe, can be safely made, that there is a definite plan of arrangement of the collecting tubules, accessory collecting tubules, when developed, and that the capillaries and flame cells are found in groups, nearly always of an equal number ^{throughout} the body. This grouping of the flame cells, naturally can occur in cercariae only where the excretory system in the cercaria approximates or

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Looss, in 1892, thirteen years after the discovery of the first flame cell in a digenetic trematode, worked out quite completely the excretory system of "Amphistomum subclavatum". In the cercaria he found the excretory system, as well as other parts, to be bilaterally symmetrical and the capillaries and flame cells to have a definite pattern. Looss (1894) also found that the excretory system of the adult worm, Allocreadium isoporum (Looss) was on a definite "2 x 6 x 4" plan; that Opisthoglyphe ranee (Froel.) was built on the "2 x 6 x 3" plan; that Haplometra cylindracea (Zeder) was also built on the "2 x 6 x 3" plan. Several others included in this paper showed a definite grouping of flame cells on each side as far as he could trace them. Sometimes the anterior end and again the posterior end would be too opaque to trace the fine capillaries. Again he found (Looss 1896) in Anchitrema sanguineum (Sons) a definite arrangement altho some of the capillary groups are in two's while others are in three's. However, in each case both sides of the body are the same. Cort (1918a, fig. 2) shows Agamodistomum mareianae (La Rue) to be built on the "2 x 10 x 6" plan. Cort (1918c, pl. VII) shows Cercariaeum mutabile to have a definite "2 x 8 x 4" plan. He (1919a) also shows Cercaria polyadena to have a definite formula, it being "2 x 6 x 3". Dollfus (1911, figs. 1 and 2) shows the excretory system of Gymnophallus somateriae Levinsen to be built on the "2 x 4 x 2" plan, and that of Cercaria pectinata Huet on the "2 x 7 x 2" plan. The Cercaria of Echinostoma revolutum is built on the "2 x 8 x 3" plan.

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Two stylet cercariae excretory systems, unpublished, that I have worked out also show a definite arrangement of the tubules and grouping of the capillaries.

When many more excretory systems have been worked out I believe that a sound classification of the families, genera, and species can be formulated if only this system is known.

However, I am not suggesting that a classification should be built upon this system only, and other similar evidence.

I believe that as more echinostome life cycles are partially or completely known that encystment in the same host will

Encysted Agamodistome or Cyst.

The cercariae of Echinostoma revolutum form encysted agamodistomes or cysts which are most commonly found in Physa occidentalis. They vary in diameter from 0.147 to 0.181 mm. but the great majority are around 0.165 mm.

Except for the numerous opaque concretions in the tubular divisions of the bladder, the agamodistome as well as the cyst wall are nearly colorless. These agamodistomes may be found encysted in any part of the body of the snail, from the foot to the extreme end of the viscera, with apparently no preference as to their location. Two hundred and eighty-two snails out of the four hundred examined or 70.5 per cent were infected with this stage. Out of the two hundred and eighty-two so infected, ninety-five or nearly 34 per cent harbored only the cyst. In this respect this species is different from the majority of digenetic trematodes in that the secondary intermediate host is the same as the intermediate host. However, Lebour (1912, p. 442) states that, "in exceptional cases the (echinostome) cercariae may encyst in its first host". Cort (1910, p. 37) finds both

Two styles of excretory systems, unpublished, that I have worked out also show a definite arrangement of the tubules and grouping of the capillaries.

When many more excretory systems have been worked out I believe that a sound classification of the families, genera, species can be formulated if only this system is known. However, I am not suggesting that a classification should be based upon this system only.

Encysted Agamodistomes or Cysts.

The cysts of Agamodistoma revivum form encysted agamodistomes or cysts which are most commonly found in Physa occidentalis. They vary in diameter from 0.147 to 0.181 mm. but the great majority are around 0.165 mm. Except for the numerous opaque concretions in the tubular divisions of the bladder, the agamodistomes as well as the cyst wall are nearly colorless. These agamodistomes may be found encysted in any part of the body of the snail, from the foot to the extreme end of the viscera, with apparently no preference as to their location. Two hundred and eighty-two snails out of the four hundred examined or 70.5 per cent were infested with this stage. Out of the two hundred and eighty-two so infested, ninety-five or nearly 34 per cent harbored only the cyst. In this respect this species is different from the majority of diogenetic trematodes in that the secondary intermediate host is the same as the intermediate host. However, Lebour (1918, p. 442) states that, "in exceptional cases the (schistosoma) cercariae may encyst in its first host". Corb (1910, p. 27) finds both

both the cercaria and cyst of Cercaria trivolvis in the tissues of Planorbis tribolois. He also found that Cercaria reflexa encysted in the same snail, Lymnaea reflexa (p. 42). Faust (1917) found Cercaria trisolenata and its cyst in the same host, occurring both in Physa gyrina and Planorbis trivolvis. He also found the cyst of Cercaria biflexa in the tissues of its host beside the Cercariae. From the above and other similar evidence, I believe that as more echinostome life cycles are partially or completely known that encystment in the same host will be found to be a common family characteristic.

It often happens that the cercariae escape from the snail only to reenter the same specimen to form the cyst. However, since 34 per cent of the snails containing cysts had only this stage, it is evident that the cercariae need not reenter the same snail from which they came. This leaving and reentering seems to be an unnecessary condition, equivalent to going up hill to go down again. It is even worse than that, since there is a decided waste of cercariae, and thus the possibility of the continuation of the life cycle is lessened. It is certainly conservative to say that many more cercariae fail to find another suitable host or ^{their} way back to the same snail than those that succeed. Such a waste of cercariae would be entirely avoided if the cercariae encysted in the same snail. Faust (1917, p. 89) found that Cercaria biflexa encysted within the host, immediately upon breaking thru the birth-pore of the redia. Such a step seems an obvious shortening likely to take place. I believe that it does take place quite often with the

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cercaria of Echinostoma revolutum. The evidence is from two sources; first, that in some cases the number of cysts exceed four hundred, while three hundred and two hundred cysts in the same snail is not uncommon. That four hundred or three hundred cercariae could find their way into a single snail from the open water seems impossible. Even for two hundred cercariae to so enter seems extremely improbable. I should say that fifty cercariae so finding entrance to one snail would be unlikely and in fact in the majority of cases less than fifty cysts are present. The second evidence is more direct, since a still further shortening of the process of encystment has been seen many times. When this shortening occurs the cercariae encyst within the rediae without ever emerging thru the birth pore. Almost by accident fifty-eight rediae were found with cysts inside, since in the great majority of snails examined no special attempt was made to see how many could be so obtained. Of these fifty-eight cysts inside rediae, twenty-six occurred singly (fig. 32), six rediae had two cysts each (fig. 33), four contained three cysts each (fig. 34) and two had four cysts each inside (fig. 35). That cercariae coming from the open water could penetrate the rediae and there encyst, two, three, or four in number is entirely impossible, in fact, that one cercaria should penetrate a redia and encyst is quite improbable. These rediae containing cysts were found in thirteen different snails. The rediae containing these cysts were of different shapes and sizes, being small, large, of normal shape or constricted at one or more places. They also differed much in color and activity. The majority

oestria of Salinostoma revolutum. The evidence is from two sources; first, that in some cases the number of oysters exceeded four hundred, while three hundred and two hundred oysters in the same shell is not uncommon. That four hundred or three hundred oestriae could find their way into a single shell from the open water seems impossible. Even for two hundred oestriae to so enter seems extremely improbable. I should say that if oestriae are finding entrance to one shell would be unlikely and in fact in the majority of cases less than fifty oysters are present. The second evidence is more direct, since a still further sorting of the products of analysis has been seen many times. When this sorting occurs the oestriae are found within the radia without ever emerging from within the pores. Almost by accident fifty-eight radia were found with oysters inside, since in the great majority of shells examined no special attempt was made to see how many could be so obtained. Of these fifty-eight oysters inside radia, twenty-six occurred singly (fig. 32), six radia had two oysters each (fig. 33), four contained three oysters each (fig. 34) and two had four oysters each inside (fig. 35). These oestriae coming from the open water could penetrate the radia and leave oysters, two, three, or four in number is entirely impossible, in fact, that one oestria should penetrate a radia and oyster is quite improbable. These radia containing oysters were found in thirteen different shells. The radia containing these oysters were of different shapes and sizes, being small, large, of normal shape or constricted at one or more places. They also differed much in color and activity. The majority

of these rediae, however, were almost lifeless and of a dark brown color. In the rediae with the cysts were sometimes found active cercariae nearly ready to escape and germ balls of different sizes.

This encysted agamodistome is not specific to Physa occidentalis since once I found it in Lymnaea traski. Also out of twenty planariae taken from the same rocks as the snails, six contained cysts, one having seventeen embedded in its muscular tissue and another ten. The other four, however, had only one, two, or three cysts. Leeches taken from the same rocks gave negative results as did the tadpoles of Hyla regilla, Baird and Girard and Notophthalmus torosus (Rathke), into whose aquaria active cercariae were placed. I predict that a thorough canvass of Stow Lake or other places where this cercaria is found would reveal other hosts for this stage. This lack of specificity of the encysted agamodistome is quite common in digenetic trematodes and is what one expects since they are in the passive state.

There are at least four ways in which the cyst may be taken into the primary host. The first and perhaps the usual way is when the infected snails being eaten by ducks, geese, etc. McAtee (1918) reports after a careful study of the food habits of seventeen hundred and twenty-five mallard ducks of the United States that 9.47 per cent of the food consists of animal matter. He says, "Mollusks, the most important element of animal food of the mallard, comprise three-fifths of this and 5.73 per cent of the total. Fresh water snails are represented most numerous no fewer than fifty sometimes

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Metaphysalis formosa (Natalis), into whose spines active
cercariae were placed. I predicted that a thorough canvass
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being taken at a single meal". That the American scaup duck, Marila marila (Linn.) eats snails is certain but the exact percentage has, so far as I know, never been tabulated. The mallard ducks eat over 90 per cent vegetable food in the wild, but it is likely that a still larger per cent is of vegetable matter in parks where they are daily fed. For this reason I should expect to find ducks living on ponds where additional food is not supplied and where the echinostome infection of snails is equally heavy, to be more parasitized with the echinostome adults than those feed in a park. The second way is that of dead snails being eaten by ducks, geese, etc. Hundreds of specimens of Physa occidentalis were seen dead on the surface of Stow Lake. Since this water is not used for drinking purposes, and thus no chemicals are used, and because there were also many healthy active snails, I feel sure that their death was caused largely by the echinostome parasites. The dead snails were found upon examination to be heavily parasitized in nearly every case. Sometimes the infection is so heavy that in quantity it is about one-third the size of the viscera of the snail. If only cysts were present, I should say little harm would be done but with an abundance of rediae also absorbing food and giving off wastes into the body, considerable injury is bound to be done and in extreme cases I believe death results. Lebour (1912, p. 423) says this concerning the effect of the parasite on the host. "The presence of sporocysts and rediae certainly injures the molluscan host. The outer appearance of the digestive gland is usually enough to show if it is inhabited by these parasites. It looks unhealthy and is a grey, sickly yellow

being taken at a single meal". That the American woodpecker, Habia melanocephala (Linn.), eats snails is certain but the exact percentage has, so far as I know, never been tabulated. The mallard ducks eat over 30 per cent vegetable food in the wild, but it is likely that a still larger per cent is of vegetable matter in parks where they are daily fed. For this reason I should expect to find ducks living on ponds where additional food is not supplied where the edmonstone infection of snails is equally heavy, to be more parasitized with the edmonstone adults than those fed in a park. The second way in that of dead snails being eaten by ducks, geese, etc. Hundreds of specimens of Physa occidentalis were seen dead on the surface of Stow Lake. Since this water is not used for drinking purposes, and thus no chemicals are used, and because there were also many healthy active snails, I feel sure that their death was caused largely by the edmonstone parasites. The dead snails were found upon examination to be heavily parasitized in nearly every case. Sometimes the infection is so heavy that in quantity it is about one-third the size of the viscera of the snail. If only eggs were present, I should say little harm would be done but with an abundance of rediae also absorbing food and giving off wastes into the body, considerable injury is bound to be done and in extreme cases I believe death results. Lebour (1912, p. 423) says this concerning the effect of the parasite on the host. "The presence of sporozoites and rediae certainly injures the molluscan host. The outer appearance of the digestive gland is usually enough to show it is inhabited by these parasites. It looks unhealthy and is a grey, sickly yellow

or a peculiar unnatural orange. It is generally completely riddled with the sporocysts or rediae which feed upon its substance. If the gonad is infected it is quite destroyed. On the other hand encysted cercariae seem to do little or no harm to their hosts even ^{though} present in large numbers."

From my own observations, and from statements by other workers I am inclined to believe Lebour is right. During the fall season of the year the dead snails are most abundant. This fact is significant in light of the fact that the rediae and cercariae are also most abundant at this time. The snails detach themselves ^{although} at death from the rocks and float to the surface, having nearly always a large part of their body extruded from the shell and thus they are very accessible as food to the water birds. Quite likely in this way many birds are infected. The third way of infection is that of the cysts being scooped up from the bottom of the pond by ducks, geese, etc. in their search for food in shallow lakes. Rediae and cercariae seldom live more than twenty-four hours in a dead snail but the encysted agamodistomes are known to live thru the decaying of the snail apparently unharmed by the putrefying process. These cysts then settle to the bottom of the pond where they remain alive for a considerable time longer unless eaten by a suitable host. A somewhat similar condition is that of the cysts of Paragonimus ringeri which break loose from the gills of the fresh water crabs and crayfish and settle to the bottom of the pond or stream. The fourth ^{although} way is that of ducks, geese, etc. eating planaria and possibly other secondary intermediate hosts. However, because the cysts were ~~two days later only five per cent~~ ^{alive, although the few remaining cysts were found in a} short time. Thus cysts in this group are in a natural condition

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fourth way is that of ducks, geese, etc. eating plants and
possibly other secondary intermediate hosts. However, because

of the heavy infection of this snail with the cysts, 70.5 per cent, I feel that the planaria and other forms of animal life play a minor role in the infection of the adult echinostome host. ~~long if in the open pond or stream, I do not~~

The cyst wall is not hard or impervious to water as was proved by accident when 5.8 per cent salt solution was used instead of normal. In each case within three minutes every cyst and of course every redia and cercariae was dead. This probably means that the cyst is absorbing moisture all the time and possibly a small amount of food. The cyst wall is round most of the time ^{although} it is capable of being changed in shape slightly, by the movement of the enclosed agamodistome.

In order to discover how long cysts could live outside the body of snails or in the tissue of dead snails, many specimens so infected were picked up at death, placed in small glass containers and examined from time to time. In the handling of the dead snails, the body wall was often ruptured and in this manner freed cysts were obtained. The water in these small glass containers was not changed but more water was added as evaporation took place. If the water had been changed occasionally, I feel sure that the cysts would have lived longer than they did because the bacteria and protozoa infection would not have been so heavy. At the end of ten days every cyst appeared to be in a healthy condition. The containers by this time had a very offensive odor. At the end of thirty-six days about 75 per cent of the cysts were alive, ^{although} in some cases part of these showed signs of deterioration. At the end of forty-two days only 11 per cent of the cysts were ~~alive~~. Two days later only five per cent were alive. ~~Evidently~~ the few remaining cysts would be dead in a short time. Thus cysts in this cramped and unnatural condition

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sometimes live longer than six weeks in dead snails and the surrounding water medium. However, for the majority their life was about five weeks. That the length of life would be twice as long if in the open pond or stream, I do not doubt in the least. These results substantiate the previous belief that cysts are quite hardy and long lived. Since this echinostome cannot encyst in water, it means that any cysts that get to the bottom of the pond must survive the decay of the snail.

Adult

Since the adult, Echinostoma revolutum, has been well described by Looss (1899), Luhe (1909), Dietz (1910) and others, very little description of this stage will be given.

The adults of Echinostoma revolutum, as previously stated, were obtained in two ways, first, by examining different species of water birds commonly found on the lake from which the snail, Physa occidentalis, was taken. One species of duck, Marila marila was found to contain three adult echinostomes in its intestine. These adults survived about fifty-five hours in the intestine of the duck, and twenty-four hours in normal salt solution. During the last twenty-four hours about forty-five eggs were produced which were incubated and traced to the full-grown miracidia stage. The second method of obtaining adults was by feeding the encysted agamodistomes (cysts) found in Physa occidentalis to mongrel ducklings which were carefully protected from other trematode infections. In this way, eight full grown worms

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and sixty-five approximately half grown worms of Echinostoma revolutum were found in the intestine. Upon careful study of the adults from both sources were found to be the same species. about 0.185 mm. in diameter while the collar of

The half grown adults 3.80 mm. long were found to have a few eggs in their uteri. and a half times larger than

Perhaps the most significant thing about the adult Echinostoma revolutum as compared with its Cercaria, is that the number of collar spines, forty-three, is not carried over in total number to the adult. The adults have only thirty-six or thirty-seven collar spines. In those with thirty-seven collar spines the last one on one of the sides is only about one-third the size of the others. In those with the thirty-six ^{spines} this small spine is lacking. This reduction in number from the cercaria to the adult, I believe, can be readily explained because of the ease with which any of the spines can be lost unless the worms are handled very carefully and the fact that there is not enough room on the collar for more spines. The spines in the adult are arranged in alternate rows as in the cercaria and also have the same clumping arrangement on the ventral side, but the number in each clump in the adult is reduced about three on a side. The size of the innermost spine, the very small one above mentioned excluded, is usually about two thirds the length of the larger ones, which are 0.099 mm. in length. Since the largest spines on the collar of the cercaria are only 0.018 mm. long this means that the majority of the collar spines have grown about five and a half times. This explains the fact above stated that there is about 0.025 mm. This is a gain of less than four and a half

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not enough room for the total number of spines on the adult collar when compared with the increase in size of the collar of the adult over the cercaria. The collar of the cercaria measures about 0.125 mm. in diameter while the collar of the adult measures but 0.495 mm. Since the collar spines of the adult are about five and a half times larger than the collar spines of the cercaria, and the size of the collar has not increased quite four times, it is obvious there would hardly be enough room for the full forty-three on the adult. This idea is further supported by the fact that the spines are arranged quite closely together on the cercaria. ~~They~~ ^{as} they measure but one third the body length. The body spines of the adult are much like those of the cercaria (fig. 45) but have increased about four times in size, those on the side between the oral and ventral suckers measuring 0.025 mm. in length. The arrangement of the body spines is about the same also. Ventrally, between the oral and ventral suckers, the spines almost completely cover the body. On the sides of the ventral sucker blunt, irregularly arranged spines were also found.

The great increase of the size of the ventral sucker is an outstanding fact. In the cercaria it is 0.094 mm. in diameter whereas in the adults 8 to 10 mm. long it averages about 1.075 mm. in diameter. The size of the oral sucker has increased on the cercaria only from 0.072 to 0.270 mm. This points to the fact that the ventral sucker in the adult plays a very important function in attachment. The distance between the oral and ventral suckers in the adult is about 1.05 mm., whereas in the cercaria it is about 0.023 mm. This is a gain of less than four and a half

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times. Since the body of the cercaria is about .5 mm. in length and the body of the adult is about 9 mm. or eighteen times larger then it is evident that the greatest region of growth of the adult body is back of the ventral sucker.

The bladder of the excretory system of the adult is interesting in that the muscular sac (1b in the cercaria) measures in length more than one-fourth the total length of the worm, whereas in the cercaria it is less than one-tenth the length of the body. The muscular tubes (1c in the cercaria) are also much elongated measuring nearly three-fifths the total length of the body of the adult whereas in the cercaria they measure but one third the body length. The concretions in the tubes of the cercaria's bladder (1d in the cercaria) are not to be found in the adult and thus the tubes are narrow only about as great in diameter as in the cercaria. The ascending tubes of the bladder (1e in the cercaria) are long in the adult as in the cercaria extending nearly the whole length of the body. Several other collecting tubules and accessory collecting tubules were also seen (fig. 49). The muscular sac division of the bladder was found to branch to either side a number of times, these branches in turn breaking up into smaller and smaller tubules that extend almost all over the body. Flame cells were never seen but the cilia in the main collecting tubule were very evident, being arranged in bunches and thus appearing much like large flame cells.

So far as the excretory system in the adult can be traced it is much like that of the cercaria, except as each part has been modified in length and size to meet its

clumping or crowding of the ventral sucker on each side is

times. Since the body of the cercaria is about 5 mm. in length and the body of the adult is about 9 mm. or slightly times larger than it is evident that the greatest region of growth of the adult body is back of the ventral sucker. The bladder of the excretory system of the adult is interesting in that the muscular sac (in the cercaria) measures in length more than one-fourth the total length of the worm, whereas in the cercaria it is less than one-fourth the length of the body. The muscular tubes (in the cercaria) are also much elongated measuring nearly three-fifths the total length of the body of the adult whereas in the cercaria they measure but one third the body length. The connections in the tubes of the cercaria's bladder (in the cercaria) are not to be found in the adult and thus the tubes are narrow only about as great in diameter as in the cercaria. The ascending tubes of the bladder (in the cercaria) are long in the adult as in the cercaria extending nearly the whole length of the body. Several other collecting tubules and accessory collecting tubules were also seen (fig. 43). The muscular and division of the bladder was found to branch to either side a number of times, these branches in turn breaking up into smaller and smaller tubules that extend almost all over the body. Flame cells were never seen but the cilia in the main collecting tubules were very evident, being arranged in bunches and thus appearing much like large flame cells. So far as the excretory system in the adult can be traced it is much like that of the cercaria, except as each part has been modified in length and size to meet its

place in the adult and the bladder is very much branched. If the flame cells, capillaries, accessory collecting tubules and collecting tubules could be accurately traced in the adult I should judge that they would be the same in number and similar in pattern. The great increase in the size of the adult over the cercaria would have to be met, so far as draining the wastes from the body is concerned, by the fine tubules of the branches of the muscular sac of the bladder.

As stated previously, Looss (1899), Luhe (1909), and others have undoubtedly placed two, perhaps more species under the name Echinostoma revolutum (= Distomum echinatum Zeder).

Looss (1899, p. 684) sums up the discussion concerning the knowledge of this species and places what I consider at least two different species together. In the first place the hosts in which he finds the two types are much different. One he finds in a shore bird of the Limicolae family, Machetes pugnax, the other type he finds in the domestic goose. If this were the only difference it would hardly be enough to make two distinct species, since specificity of hosts is probably not as great as usually indicated. But on examination the number of collar spines is found to be entirely different in number. The one found in the goose, he shows to have thirty-seven spines, while the other from the shore bird to have but thirty-four spines. Furthermore the length, the shape and the arrangement of the spines are entirely different. In one the smaller inner spines are not present while the other has them. The clumping or crowding of the ventral spines on each side is

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place the hosts in which he finds the two types are much
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to be found in one and not the other. The range of variation in egg size is also different. One range of variation is from 0.092 to 0.134^{mm.}/the other from 0.101 to 0.111 mm.

Since Echinostoma revolutum was first found by Froelich in the goose, and later by Zeder, Looss in the goose and duck and by others and myself, the type with the thirty-seven spines, I think, should be called by the above name and a new name chosen for the one with the thirty-four spines found in the shore bird, Machetes pugnax. I suggest the name Echinostoma limicoli. The large number of primary hosts assigned to this species by different workers I feel quite sure is due to placing two or more species under the one name.

Theoretical Discussion of the Life Cycle.

Briefly stated the stages of the life cycle of Echinostoma revolutum are these: egg miracidium, mother-redia, daughter-redia, cercaria, encysted agamodistome (cyst) and adult. To accomplish this life cycle only two hosts are necessary, the snail Physa occidentalis and a duck or goose. Apparently any duck and perhaps any goose forms a suitable host, since the adult echinostomes were raised experimentally in mongrel ducklings, were found in the American scaup duck, Marila marila on Stow Lake and have been reported from many other ducks and geese in many places in the northern hemisphere. As stated, Physa occidentalis usually serves as both the intermediate and secondary intermediate host. This echinostome, however, is not specific since the encysted agamodistome stage has also been found in another species of snail and planaria.

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Theoretical Discussion of the Life Cycle.

Bristly stated the stages of the life cycle of Echinostoma revolutum are these: egg, miracidium, mother-tadpole, daughter-tadpole, cercaria, encysted acanthostome (oyst) and adult. To accomplish this life cycle only two hosts are necessary, the snail Physa occidentalis and a duck or goose. Apparently any duck and perhaps any goose forms a suitable host, since the adult Echinostomes were raised experimentally in manure. ducklings, were found in the American house duck, Mallus mallus on Star Lake and have been reported from many other ducks and geese in many places in the northern hemisphere. As stated Physa occidentalis usually serves as both the intermediate and secondary intermediate host. This Echinostome, however, is not specific since the encysted acanthostome stage has also been found in another species of snail and planaria.

Although all the stages in the life cycle have been found and the necessary hosts are known, yet the time of the appearance of each stage and its duration is not known.

In regions where there is a definite winter or freezing period, I believe, each stage will be found during a certain season of the year. In the San Francisco bay region of California where light frosts may sometimes occur, the seasonal distribution of each stage is hard to solve. For this reason, California is not a good place to work on this particular part of the problem of the life cycle, although very favorable in every other respect. I would expect and do find here considerable overlapping of the stages taking place.

During the migration of water birds in the spring and fall seasons of the year, the great majority of the eggs are doubtless vented in California ponds and streams. Although some few ducks and geese nest in the bay region of California, and thus some eggs are probably vented in the summer time also, yet the great majority of the ducks and geese raise their young farther north. If the eggs are vented into the ponds and streams during the fall migration, the eggs doubtless remain practically dormant during the winter season. This conclusion is reached because the temperature of the water, altho seldom at the freezing point, yet is sufficiently low to keep the germ balls in the redia from developing. This conclusion is borne out by the work of Nakagawa (1917) in connection with the development of the eggs of Paragonimus westermanni Kerbert. He makes this statement concerning the incubation period

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of these eggs. "The rate of development of the miracidia varies with the temperature and is retarded by cool weather. During the summer in Shinchiku (Formosa) i.e., from May to October, the melon seed-like miracidia develop in 14 to 15 days, begin to move in 19 to 22 days, and hatch in 23 to 28 days. In March and April they take some weeks to hatch, and the miracidia remain for a long time within the egg even tho they are as lively as in the warm season. From November to February or March no development was noted, tho the eggs were watched constantly. According to my observations, the temperature for hatching is $25 - 31^{\circ} \text{C}$, and embryonic development ceases below 25°C . Manson gives $26-34^{\circ} \text{C}$., Nakahama 30° ., and Garrison and Leynes $25-34^{\circ} \text{C}$. At 37°C . the eggs seem to disintegrate". If the eggs are vented during the spring migration, doubtless they begin development immediately. Thus the egg produced during the fall and spring seasons of the year would develop into miracidia at about the same time. These miracidia, I should expect to appear about the first to the middle of May. By the process of metamorphosis and growth the mother-rediae should have daughter-rediae inside ready to escape thru the birth pore by the middle of July. These daughter-rediae in turn, I should expect to have grown to maturity and to have cercariae escaping thru the birth pore by the middle of August or the first of September. This more rapid development of the daughter-rediae than the mother-rediae, I should expect, because of the warmer weather for the former. From the middle of August until

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November the cercariae are known to develop rapidly and to be continually escaping from the daughter rediae to form cysts in other snails or planaria or to return to the same snail. Since many cercariae do not leave the snail but encyst just after emerging from the birth pore of the redia, some encysted agamodistomes are certain to be formed. Also since from September to November is the fall migration season, it is clear that the cysts are formed just in time to be eaten with the snails by migrating ducks and geese.

As shown by experimental feeding of encysted agamodistomes to young ducklings, the mature adult echinostomes appear in four weeks, having at this time about five hundred eggs in the uterus. In the winter home of the ducks and geese, numerous eggs undoubtedly are being given off. This explains the fact that Echinostoma revolutum, in the various stages, could be found far south, as no doubt it is.

The adult worms doubtless live for several years in the intestine of the ducks and geese, producing eggs all the while. The length of life of this adult echinostome could easily be determined by feeding the cysts to young ducklings and examining the feces from month to month.

Altho the mother-rediae stage doubtless can be found during any season of the year in California, yet the winter season is probably its dormant period as will be proved in case of the daughter-rediae. Even though probably found during any season of the year in Californ, because some ducks and geese stay the year round, yet as stated before, I should

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The daughter-rediae stage, i.e., the rediae producing cercariae/seasons of the year in California, yet it is found most abundantly in the fall. That the germ balls grow little or none during the months of December, January, February, and March is evidenced by the fact that during the sixty-three days from December 6th to February 7th, not a single cercaria was to be found, and from February 7th to the first of April they were very rarely seen, altho the rediae were abundant. The temperature of the water is probably the controlling factor. The temperature of water of three lakes about the size of Stow Lake has been kept daily for several years. These three lakes are close to Stow Lake and are about the same size so that their temperature probably differs but little. During the three winter months the average temperature of the water is 52°F, occasionally dropping as low as 48°F. Beginning the first of March there is ^a quite rapid and steady rise in the temperature which is accompanied by a corresponding increase in the number of active cercariae. During the three warmest months, July, August, and September the temperature averages 67°F, occasionally reaching 70°F. During these three months and the month following the active cercariae continually increase in number. It seems obvious that the degree of temperature controls the development of cercariae and possibly of mother-rediae and the enclosed daughter-rediae

expect to find this stage most abundant during May, June, and July. The daughter-redia stage, i.e., the redia proper, is known to exist at all during certain seasons of the year in California, yet it is found most abundantly in the fall. That the germ balls grow little or none during the months of December, January, February, and March is evidenced by the fact that during the sixty-three days from December 6th to February 7th, not a single cercaria was to be found, and from February 7th to the first of April they were very rarely seen, although the rediae were abundant. The temperature of the water is probably the controlling factor. The temperature of water of three lakes about the size of Snow Lake has been kept daily for several years. These three lakes are close to Snow Lake and are about the same size so that their temperature probably differs but little. During the three winter months the average temperature of the water is 52°F , occasionally dropping as low as 48° . Beginning the first of March there is a rapid and steady rise in the temperature which is accompanied by a corresponding increase in the number of active cercariae. During the three warmest months, July, August, and September the temperature averages 67°F , occasionally reaching 70° . During these three months and the month following the active cercariae continually increase in number. It seems obvious that the degree of temperature controls the development of cercariae and possibly of mother-rediae and the enclosed daughter-rediae.

There are four ways by which stages other than the adult of Echinostoma revolutum can pass through the so-called winter season in the bay region of California. The first way is by means of the egg. The second way is by means of the mother-redia. This could only result from eggs being produced during the late summer, or early fall. During the process of metamorphosis from the miracidia into the mother-redia, or after the enclosed daughter-redia had grown nearly to full size, the coming of winter would force the mother-redia to remain dormant until spring. The third way is by means of the daughter-rediae, i.e., rediae containing cercariae. This could result only from eggs produced during mid-summer. The following table gives an analysis of the various stages of Echinostoma revolutum found in the four hundred and nearly enough time for the daughter-rediae to produce active cercariae. The lack of time to mature the cercariae would force the daughter-rediae to remain dormant until spring. The fourth way is by means of the encysted agamodist. In a climate where there is a definite winter season, I doubt if the second and third ways of surviving the winter exist.

The length of life of echinostome rediae has never been determined, but doubtless they exist for a year or more. The reason for this conclusion is, that since the average number of active cercariae in the rediae is five, and the total number of germ balls of all sizes is over a hundred, probably closer to two hundred, it seems impossible that all the germ balls could grow to maturity in less than a year's time. That they exist in a dormant or semi-dormant condition for the four months of the winter season is known.

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How long an encysted agamodistome may live in a living snail has also never been determined. Since cercariae are not produced during the winter months, and since cysts are found thruout the year, it is obvious that they live for at least four months. Doubtless they exist for a year and perhaps several years in the tissues of the snail. as previously stated, is due to this snail being both the intermediate and secondary intermediate host.

Physa occidentalis in aquaria and by placing with these young snails the cercariae of Echinostoma revolutum, the duration of the cyst could be determined by examination of the snails from month to month.

The following table gives an analysis of the various stages of Echinostoma revolutum found in the four hundred snails of various ^{size of} Physa Occidentalis taken from Stow Lake, Golden Gate Park, San Francisco:

Mother-rediae.....	13
Daughter-rediae and cercariae.....	234
Encysted agamodistomes or cysts.....	282
Cysts only.....	95
Cysts within rediae.....	13
Uninfected snails.....	53

These snails were examined during every month of the year except July. The cyst and daughter-redia stages were found during every month but the mother-redia stage was found only in the months of December, January and February. Since the mother-redia stage was not known or even suspected until December 1918, it is obvious that more than thirteen snails were so infected. Also, since as stated, no effort was made to see if all the snails

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The following table gives an analysis of the various stages of Lophomonas reuteri found in the four hundred snails of various Physa coelenteralis taken from Snow Lake, Golden Gate Park, San Francisco:

Uninfected snails.....	13
Cysts only.....	234
Cysts within rediae.....	232
Uninfected snails.....	13
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had some rediae that contained cysts, the number so parasitized was also probably much greater than recorded. The outstanding feature of the above table is that such a large percentage of Physa occidentalis contained some stage of the parasite. Perhaps the next most important feature is that more snails were found to be infected with cysts than with rediae. This, as previously stated, is due to this snail being both the intermediate and secondary intermediate host.

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Explanation of Plates.

Explanation of Plates.

Abbreviations.

- 1a Caudal division of bladder.
- 1b Muscular sac of bladder.
- 1c Muscular descending tube of bladder.
- 1d Concretional descending tube of bladder.
- 1e Ascending tube of bladder.
- 2a, 2b, 2c, 2d Collecting tubules.
- 3a, 3b, 3c, 3d, 3e, 3f, 3g, 3h Accessory collecting tubules.
- 1-24 Flame cells
- ac Acetabulum.
- ap Anterior papilla.
- bp Birth pore.
- c Cercaria
- cgb Cercaria germ ball
- ens Central nervous system
- es Collar spines
- dr Daughter-redia
- drgb Daughter-redia germ ball
- ec Excretory concretions
- ep Excretory pore
- es Esophagus
- gp Genital pore
- i Intestine
- ir Intestine of redia
- o Ovary
- os Oral sucker
- ov Oviduct
- p Pharynx
- T₁, T₂, Testes
- u Uterus
- vd Vitelline duct
- vg Vitelline glands
- vn Vitelline reservoir

Explanation of Plates.

Abbreviations.

1a	Caudal division of bladder.
1b	Muscular sac of bladder.
1c	Muscular descending tube of bladder.
1d	Concretional descending tube of bladder.
1e	Ascending tube of bladder.
2a, 2b, 2c, 2d	Collecting tubules.
3a, 3b, 3c, 3d, 3e, 3f, 3g, 3h	Accessory collecting tubules.
1-24	Plasma cells.
ac	Acetabulum.
ap	Anterior papilla.
bp	Birth pore.
c	Cervix.
cdp	Cervix germ ball.
ens	Central nervous system.
es	Collar spines.
dr	Daughter-redia.
drdp	Daughter-redia germ ball.
ec	Excretory concretions.
ep	Excretory pore.
es	Esophagus.
gp	Genital pore.
p	Pharynx.
tr, tg, testes	Testes.
u	Uterus.
vd	Vitelline duct.
vg	Vitelline glands.
vr	Vitelline reservoir.
ov	Oviduct.
os	Oral sucker.
o	Ovary.
ir	Intestine of redia.
i	Intestine.

- Fig. 30. Explanation of Plates. daughter-redia. x 315
- Fig. 31. Mature daughter-redia showing excretory system.
x 36. Plate I.
- Fig. 32. Mature daughter-redia containing one encysted
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- Fig. 17. Egg just after escape of miracidium showing
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agamodistomes. x 44.
- Fig. 18. Eggshell with operculum detached. x 34
- Fig. 34. Mature daughter-redia containing three encysted
Fig. 18a. Operculum of egg. x 34.
agamodistomes and germ balls. x 76.
- Fig. 35. Mature Plate II. redia containing four encysted
agamodistomes, two mature cercariae and a germ
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- Fig. 36. Mature daughter-redia containing one mature
Fig. 20. Immature mother-redia. x 429.
- Fig. 21. Immature mother-redia. x 333.
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three mature cercariae and several germ balls.
- Fig. 22. Immature daughter-redia contracted. x 372.
x 60.
- Fig. 23. Immature daughter-redia extended. x 372.
- Fig. 24. Anterior end of mature daughter-redia extended
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- Fig. 37. Cercaria germ-ball showing beginning of excretory
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- Fig. 38. Cercaria germ-ball showing formation of tail and
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- Fig. 39. Further development of cercaria. Note bulb-like
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- Fig. 28. Lateral view of daughter-redia just after
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- Fig. 29. Immature daughter-redia with germ balls inside
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Plate I.

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 Fig. 18. Eggshell with operculum detached. x 34
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Plate II.

- Fig. 19, 20, 21, 22, 23, 24. Mother-redia in various stages of extension
 x 429.
 Fig. 20. Immature mother-redia. x 429.
 Fig. 21. Immature mother-redia. x 333.
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 Fig. 23. Immature daughter-redia extended. x 372.
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 x 140.
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 and germ balls. x 118.
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- Fig. 28. Lateral view of daughter-redia just after
 escape from mother-redia. x 446.
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- Fig. 30. Flame cell of mature daughter-redia. x 313
- Fig. 31. Mature daughter-redia showing excretory system. x 66.
- Fig. 32. Mature daughter-redia containing one encysted agamodistome (cyst) and germ balls. x 49.
- Fig. 33. Mature daughter-redia containing two encysted agamodistomes. x 44.
- Fig. 34. Mature daughter-redia containing three encysted agamodistomes and germ balls. x 76.
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- Fig. 36. Mature daughter-redia containing one mature tetracotyle, several immature tetracotyle, three mature cercariae and several germ balls. x 60.

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- Fig. 37. Cercaria germ-ball showing beginning of excretory system. x 190.
- Fig. 38. Cercaria germ-ball showing formation of tail and further development of excretory system. x 190.
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Fig. 38.	Cercariae germ-ball showing formation of tail and further development of excretory system. x 190.
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Plate VI.	
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Fig. 51.	Further development of excretory system. x 22.
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Fig. 53.	Further development of excretory system. x 22.
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Fig. 55.	Further development of excretory system. x 22.
Fig. 56.	Further development of excretory system. x 22.
Fig. 57.	Further development of excretory system. x 22.
Fig. 58.	Further development of excretory system. x 22.
Fig. 59.	Further development of excretory system. x 22.
Fig. 60.	Further development of excretory system. x 22.
Fig. 61.	Further development of excretory system. x 22.
Fig. 62.	Further development of excretory system. x 22.
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